Environmental Causes and Physiological Consequences of Social Flexibility: a Field Study in the African Striped Mouse (*Rhabdomys pumilio*)

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Summary

Social organization in animals is varied and ranges from solitary to group-living. Differences in social organization between species are believed to arise as a consequence of differences in their ecology, social behaviour, and physiology. To understand social organization it is important to study both the ultimate and the proximate factors that lead to group- or solitary-living in an integrative way. While the reasons for group-living have been extensively studied in the field and described in the literature, little is known about why individuals choose to become solitary. Furthermore, the behavioural and physiological differences between the two forms of social organisation are not well understood. In my PhD thesis I used a multidisciplinary approach to investigate this topic, by studying the socially flexible African striped mouse (*Rhabdomys pumilio*). Striped mice are an ideal species to address the environmental, physiological and behavioural factors determining the two different forms of sociality as they can be group- or solitary-living, with both occurring within the same population and at the same time.

I first investigated the environmental causes of group- and solitary-living. Group-living can arise as a consequence of ecological constraints (i.e. when population density is high and resources, such as free territories are scarce), while reproductive competition between group members leads to increased costs of group-living, and thus promotes solitary-living. Several observational and some experimental studies have confirmed the "ecological constraints" hypothesis, but to date no studies have been able to show experimentally whether reproductive competition can explain solitary-living. I tested ecological constraints measured as population density by using a field manipulation experiment, in which I removed groups of striped mice and created vacant territories for neighbouring mice. I investigated whether dispersal and solitary-living were more likely to occur when reproductive competition was present, by replicating my experiments during both the breeding and the non-breeding season. My experiments support the ecological constraints hypothesis as when groups were experimentally removed, more striped mice from groups directly neighbouring the removed groups moved into the vacant territories and became solitary than striped mice from control groups not neighbouring removed groups. Most importantly, I was able to show experimentally for the first time that reproductive competition can explain solitary-living, as significantly more striped mice became solitary during the breeding than during the non-breeding season, when individuals remained group-living despite the availability of free territories.

In a second study, I addressed the behavioural differences between group- and solitary-living individuals. Using a series of dyadic encounter tests in a neutral presentation arena, I tested whether mice that became solitary would be more aggressive, less amicable and more investigative than individuals that remained group-living. Further I was interested to know whether differences between group-living and solitary individuals were a product of an individual personality or arose as a consequence of tactic change. Solitary striped showed higher levels of aggression and social investigation than their conspecifics that remained group-living, differences that were already present before individuals dispersed and changed from a group-living to a solitary tactic. I found the behaviour of dispersing mice to be consistently different from the behaviour of mice that remained group-living, suggesting that differences in personality traits among individuals influence their dispersal capabilities. While individuals with a specific personality (e.g. more aggressive)

might be more likely to disperse and become solitary, it is ultimately the environment that provides the conditions that allow individuals to switch their social tactics.

In a third study, I examined the physiological differences of group- and solitary-living. Studies of species with alternative reproductive tactics have shown that individuals following different tactics differ in their steroid hormone levels. To determine whether differences in social tactic correlated with hormonal differences, I collected blood samples from solitary and group-living individuals before and after the former changed tactic. As reproductive suppression and social stress typically lead to higher corticosterone and lower testosterone levels, I specifically looked at the role of these two hormones. Solitary striped mice of both sexes had significantly lower corticosterone levels than group-living individuals. Solitary males – but not solitary females – had higher testosterone levels than group-living conspecifics, thus supporting the hypothesis that group-living results in physiological stress and can induce reproductive suppression in both sexes.

In a final study, I investigated the effects that resource availability and population density have on home range sizes and overlap. As recourse availability and population density are often correlated with each other, it is important to address the effects that they play on home range patterns independently to be able to estimate which one of the two is the most important factor. I used two separate field manipulation experiments in which I tested for the role of those two factors separately while I controlled for the other. In the first experiment I manipulated food availability by providing additional food and controlled for population density by restricting immigration and recruitment. In the second experiment I manipulated population density by removing groups of mice and controlled for food availability by performing the study within a short time period during the breeding season when food is most abundant. I restricted my study to adult breeding females, to avoid sex- and age-biases. In accordance with results obtained for other species, I found home range sizes of female striped mice to be negatively affected by the provisioning of additional food (20% decrease) and positively affected by the removal of neighbouring individuals (40% increase). In contrast with previous findings, however, female striped mice did not shift their home range but mostly used the same area throughout the study. The number and the sex of neighbouring individuals were also found to be important in regulating home range sizes and overlap of females.

Overall, with my PhD project I was able to show that individuals become solitary to avoid reproductive competition, but remain group-living when ecological constraints are high or when no reproductive competition occurs. Further, I was able to demonstrate that solitary individuals differ behaviourally and physiologically from group-living individuals, and that behavioural differences are already present before a new tactic is adopted. Additionally, I was able to separate the effects that population density and food resources play on animal space used patterns. Thus, by using an experimental approach and therefore demonstrating causation of results previously mostly described correlatively in observational studies, my research significantly contributed to better understanding the physiological, behavioural and environmental factors that are responsible for the variation in social organization.

Zusammenfassung

Soziale Organisation bei Tieren ist vielseitig; Individuen können entweder in einer Gruppe oder solitär leben. Unterschiede in der sozialen Organisation zwischen Arten sind auf Unterschiede in ihrer Ökologie, ihrem sozialem Verhalten und ihrer Physiologie zurückzuführen. Um soziale Organisation zu verstehen, ist es wichtig sowohl die ultimaten wie auch die proximaten Ursachen auf verschiedenen biologischen Ebenen zu untersuchen, die Individuen dazu veranlassen in Gruppen oder solitär zu leben. Während die Ursachen einer sozialen Lebensweise schon umfangreich im Feld untersucht und in der Literatur beschrieben wurden, weiss man wenig darüber, warum Individuen eine solitäre Lebensweise wählen. Zudem werden die Verhaltens- und physiologischen Unterschiede zwischen den zwei Formen sozialer Organisation nicht gut verstanden. In meiner Doktorarbeit wandte ich einen multidisziplinären Ansatz an, um dieses Thema zu erforschen, indem ich die sozial flexible Afrikanische Striemengrasmaus (*Rhabdomys pumilio*) studierte. Striemengrasmäuse sind eine ideale Art, um die Umwelt-, physiologischen und Verhaltensfaktoren zu untersuchen, welche die zwei Formen sozialen Verhaltens bestimmen. Sie können in derselben Population zur gleichen Zeit sowohl in Gruppen wie auch solitär leben.

Als Erstes untersuchte ich die Umweltfaktoren, die ein Individuum veranlassen in der Gruppe oder solitär zu leben. Eine soziale Lebensweise kann als Folge von Umwelteinschränkungen (z.B. bei einer hohen Populationsdichte und einem Mangel an Ressourcen, wie freie Territorien) entstehen. Dagegen erhöht ein Fortpflanzungswettbewerb zwischen Gruppenmitgliedern die Kosten einer sozialen Lebensweise und fördert somit eine solitäre Lebensweise. Mehrere Beobachtungsstudien und einige experimentelle Studien haben die “ecological constraint“ Hypothese bestätigt. Bisher konnte noch keine Studie experimentell zeigen, dass Fortpflanzungswettbewerb der Grund für eine solitäre Lebensweise ist. Ich untersuchte Umwelteinschränkungen, gemessen an der Populationsdichte, indem ich ein Manipulationsexperiment im Feld durchführte. In diesem Experiment entfernte ich Gruppen von Striemengrasmäusen und erzeugte so leer stehende Territorien für die Nachbarsmäuse. Ich untersuchte, ob Abwanderung und eine solitäre Lebensweise öfters auftraten bei einem vorhandenen Fortpflanzungswettbewerb, indem ich meine Experimente während und ausserhalb der Fortpflanzungssaison wiederholte. Meine Experimente unterstützen die „ecological constraint“ Hypothese; wenn Gruppen experimentell entfernt wurden, wanderten mehr Striemengrasmäuse, aus der direkten Nachbarschaft der entfernten Gruppen, in die freistehenden Territorien ab und wurden solitär. Die Striemengrasmäuse der Kontrollgruppen waren keine Nachbarn der experimentell entfernten Gruppen und wanderten als Folge weniger häufig ab. Ich konnte als Erste experimentell zeigen, dass ein Fortpflanzungswettbewerb eine solitäre Lebensweise erklären kann. Denn signifikant mehr Striemengrasmäuse wurden solitär während der Fortpflanzungssaison als ausserhalb, wenn Individuen weiterhin in Gruppen lebten trotz freier Territorien.

In einer zweiten Studie befasste ich mich mit den Unterschieden im Verhalten zwischen sozialen und solitären Individuen. Ich benutzte eine Reihe von dyadischen Begegnungstests auf einem neutralen Präsentationsgelände. Dort testete ich, ob Mäuse, welche solitär wurden, aggressiver, weniger freundlich und neugieriger waren als solche, die in der Gruppe blieben. Des Weiteren war ich daran interessiert herauszufinden, ob Unterschiede zwischen gruppenlebenden und solitären Individuen

auf eine individuelle Persönlichkeit zurückzuführen sind oder eine Folge einer Strategieänderung waren. Solitäre Striemengrasmäuse zeigten höhere Aggressionswerte und erforschten ihre Partner häufiger als Artgenossen, die weiterhin in der Gruppe lebten. Diese Unterschiede waren schon vorhanden bevor die Individuen abwanderten und von einer sozialen zu einer solitären Strategie wechselten. Ich fand heraus, dass das Verhalten von abwandernden Mäusen sich durchwegs von den Mäusen unterscheidet, die in der Gruppe verweilten. Dies lässt darauf schliessen, dass unterschiedliche Charaktermerkmale von Individuen ihr Abwanderungsverhalten beeinflussen. Während Individuen mit einer spezifischen Persönlichkeit (z.B. höhere Aggressivität) vielleicht mit einer höheren Wahrscheinlichkeit abwandern und solitär werden, liefert schlussendlich die Umwelt die Voraussetzungen dafür eine soziale Strategie zu ändern.

In einer dritten Studie untersuchte ich die physiologischen Unterschiede zwischen einer solitären und einer sozialen Lebeweise. Studien über Arten mit einer alternativen Fortpflanzungsstrategie haben gezeigt, dass Individuen mit unterschiedlichen Strategien, verschiedene Steroidhormonwerte aufweisen. Ich sammelte Blutproben von solitären und gruppenlebenden Individuen, vor und nach einem erfolgten Strategiewechsel, um zu bestimmen, welche Unterschiede in der sozialen Strategie mit Hormonunterschieden korrelieren. Da Unterdrückung in der Fortpflanzung und sozialer Stress typischerweise zu höheren Kortikosteron- und tieferen Testosteronwerten führt, prüfte ich insbesondere die Rolle von diesen zwei Hormonen. Solitäre Striemengrasmäuse beider Geschlechter hatten signifikant tiefere Kortikosteronwerte als gruppenlebende Individuen. Solitäre Männchen, jedoch nicht solitäre Weibchen, hatten höhere Testosteronwerte als ihre gruppenlebenden Artgenossen. Dies unterstützt die Hypothese, dass eine soziale Lebensweise zu physiologischem Stress und Unterdrückung der Fortpflanzung bei beiden Geschlechtern führen kann.

In einer letzten Studie untersuchte ich den Einfluss von Ressourcenverfügbarkeit und Populationsdichte auf die Territoriumsgrösse und deren Überlappung. Da Zufluchtmöglichkeit und Populationsdichte häufig miteinander korrelieren, ist es wichtig sich mit der deren Effekt auf die Territoriumsstruktur zu befassen. Auf diese Weise kann man herausfinden, welcher der zwei Faktoren wichtiger ist. Ich verwendete zwei getrennte Manipulationsexperimente im Feld, in denen ich die Rolle dieser zwei Faktoren getrennt prüfte, während der andere Faktor als Kontrolle diente. Im ersten Experiment manipulierte ich die Futterverfügbarkeit indem ich zusätzliches Futter zur Verfügung stellte. Darüber hinaus kontrollierte ich für die Populationsdichte indem ich Einwanderung und Rekrutierung einschränkte. Im zweiten Experiment manipulierte ich die Populationsdichte dadurch dass ich Mäusegruppen entfernte. Ich kontrollierte für Futterverfügbarkeit indem ich die Studie während einer kurzen Zeitspanne in der Fortpflanzungssaison durchführte, wenn Futter am häufigsten vorkommt. Ich begrenzte meine Studie auf adulte Zuchtweibchen, um Geschlechts- und Alters Effekte ausschliessen zu können. In Übereinstimmung mit Resultaten von Studien über andere Arten, fand ich heraus, dass die Territoriumsgrösse von weiblichen Striemengrasmäusen negativ beeinflusst wird durch die Verfügbarkeit von zusätzlichem Futter (20% Verkleinerung) und positiv durch die Entfernung von Nachbarsindividuen (40% Vergrösserung). Im Unterschied zu früheren Ergebnissen wechselten die weiblichen Striemengrasmäuse ihr Territorium nicht, sondern benutzten mehrheitlich dasselbe Areal während der gesamten Studie. Die Anzahl und das Geschlecht der Nachbarsindividuen waren

ebenfalls wichtig in der Regulation der Territoriumsgrösse und bei Überschneidungen der Territorien von Weibchen.

Insgesamt konnte ich mit meiner Doktorarbeit zeigen, dass Individuen solitär werden, um Fortpflanzungswettbewerb zu vermeiden, jedoch in der Gruppe blieben, wenn die Umwelteinschränkungen hoch waren oder keine Konkurrenz um Fortpflanzung stattfindet. Ausserdem konnte ich demonstrieren, dass solitäre Individuen sich sowohl im Verhalten wie auch in ihrer Physiologie von gruppenlebenden Individuen unterscheiden und dass Unterschiede im Verhalten schon vor dem Strategiewechsel vorhanden waren. Zusätzlich konnte ich die Effekte der Populationsdichte und Futterverfügbarkeit auf die Territoriumsnutzung voneinander unterscheiden. Ich verwendete Experimente, um die Resultate aus früheren Beobachtungsstudien zu unterstützen und die zugrunde liegenden Mechanismen besser zu erfassen. Meine Forschung trägt erheblich dazu bei die physiologischen, Verhaltens- und Umweltfaktoren besser zu verstehen, die zu Variationen in der sozialen Organisation führen.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

1. BACKGROUND

Social organization in animals is variable and includes species that live solitarily, species that form single families, extended families and even eusocial species with distinct casts (Blumstein and Armitage 1999; Burda *et al.* 2000; Balshine *et al.* 2001; Clutton-Brock 2005). While the reasons for group-living have been extensively studied (Krebs and Davis 1993; Emlen 1994; Hatchwell and Komdeur 2000), the reasons for solitary-living have, in comparison, received less attention. Yet to understand why species show such staggering variety in social organizations we must not only consider why social groups form, but also why individuals choose to live solitarily (Hamilton 1964, Wilson 2000).

Most commonly, social groups form when adult offspring delay dispersal and remain in the natal group (Axelrod and Hamilton 1981, Alcock 2001, Baglione *et al.* 2005). Such groups typically consist of breeding and subordinate non-breeding individuals. Subordinate in such groups are the sons or daughter of the breeders, which sometimes act as helpers at the nest, and experience both direct and indirect fitness benefits (Hamilton 1964; Brown 1987, Krause and Ruxton 2002). However, remaining as a subordinate non-breeding helper also entails costs. Individuals that defer dispersal and remain within their natal group after having reached sexual maturity often have to deal with costs associated with reproductive competition, which can lead to intra-group conflict and sexual suppression (Emlen 1997; Brant *et al.* 1998; Clutton-Brock 2005). Thus, in addition to costs typically associated with group-living (e.g. competition for limited food resources; enhanced susceptibility to parasites, etc.), philopatric non-breeding subordinates may experience extra costs: i) by delaying onset of their own reproduction, and by ii) performing costly helping behaviour (MacColl and Hatchwell 2002). Reproductive competition could, therefore, be seen as the primary factor promoting dispersal and solitary-living in subordinate non-breeders; yet, in many social species, individuals remain natally philopatric. What circumstances would, thus, determine when an individual remains philopatric or it becomes solitary?

Individuals are expected to delay dispersal only when the benefits of staying at home range (i.e. remaining philopatric) outweigh the benefits of dispersing and becoming

solitary. The ecological constraints hypothesis, also known as "the habitat saturation model", predicts that offspring will remain philopatric when opportunities for independent breeding are scarce, e.g. when no vacant territories are available, which typically occurs when population density is high (Emlen 1982a, b, 1994; Koenig *et al.* 1992). Ecological constraints reduce benefits of dispersal and thus favour philopatry (Stacey and Ligon 1991). In sum, ecological constraints may favour group-living, while reproductive competition might favour solitary-living.

While avoidance of intra-group conflict resulting from reproductive competition has been used as a plausible explanation as to why animals disperse and become solitary (Emlen 1982a), these factors are more difficult to test empirically than ecological constraints. While several removal experiments in the field have already shown that individuals delay dispersal when habitats are saturated and resources are limited (Pruett-Jones and Lewis 1990; Komdeur 1992; Lucia *et al.* 2008), no study so far has been able to successfully show empirically that reproductive competition leads to solitary-living. One way to test for the effect of reproductive competition on dispersal decisions and sociality is to compare between periods with and without reproductive competition, which could be achieved by using a seasonally breeding species with year round territoriality.

For seasonal species, the costs associated with reproductive competition only exist during the breeding season; and thus the fitness consequences of group-living are expected to be different during the breeding and the non-breeding season (Johnstone *et al.* 1999; Hatchwell and Komdeur 2000). Specifically, offspring are expected to remain philopatric towards the end of the breeding season when reproductive competition ceases and, hence, there are no costs associated with delayed dispersal. In contrast, offspring are expected to disperse at the beginning of the breeding season, when reproductive competition is high and the costs of remaining group-living outweigh its benefits.

Thus, when ecological constraints are relaxed and reproductive competition is present, it is expected that individuals will disperse and become solitary. Understanding the effects that ecological constraints and reproductive competition bear on individuals' behaviour is critical in explaining the social organization of populations and species (Emlen and Oring 1977; Hayes *et al.* 2007). Several studies have shown that spacing

behaviour of individuals can be correlated with both resource availability and population density. For example, individuals' home range tend to decrease when additional food is provided (Ims 1987; Roth and Vetter 2008) and to increase when neighbours are experimentally removed (Norman and Jones 1984; Boutin and Schweiger 1988; Baker *et al.* 2000). Thus it would be important to understand which ecological factor is the most important in determining space use patterns in animals as this may ultimately affect the social organization of a population as a whole (Wang *et al.* 2011).

It is, also, unclear whether these external environmental conditions force individuals to behave differently as they switch from group-living to solitary or whether individuals are behaviourally predisposed to disperse and become solitary when conditions are optimal, and, if so, how this is regulated proximately. Individuals of solitary species are though to differ behaviourally and physiologically from individuals of group-living species. Within the social context, for instance, individuals of solitary species rarely interact with their conspecifics (Lacey and Wierczorek 2003), whereas individuals of group-living species remain together for prolonged periods of time, interacting frequently and extensively with members of their own group (Wilson 2000). Further, it has been shown that individuals following alternative reproductive tactics display distinct physiological profiles (Oliveira *et al.* 2008), thus it is expected that individuals following different social tactic might also differ. Hormones, in particular, are thought to play a prominent role as they can act directly in the brain and on the peripheral organs and, hence, affect behaviour (Butin 1996).

Therefore, to understand social organization it would be important to study both the ultimate and the proximate factors that lead to group- and solitary-living, yet, no study so far has been able to address this topic in an integrative way, and the behavioural and physiological factors underlining group- and solitary-living remain largely poorly understood. The reasons behind this could be that comparisons between individuals of solitary and group-living species are difficult to make without encountering phylogenetic bias. One way to circumvent this problem would be to compare ecological, behavioural and physiological profiles of individuals belonging to socially flexible species. Individuals of socially flexible species are able to switch between alternative reproductive tactics according to changing environmental conditions (Schradin *et al.* 2012). In socially flexible species, both group- and solitary-living

individuals can occur within the same population (Schradin *et al.* 2012). Socially flexible species thus provide unique model organisms to understand the factors leading to group- or solitary-living.

2. STUDY SPECIES

The African striped mouse (*Rhabdomys pumilio*) is a socially flexible species (Schradin *et al.* 2012). In the Succulent Karoo of South Africa, striped mice of both sexes are able to follow one of three different alternative reproductive tactics: 1. they can remain as philopatric non-breeding helpers in their natal group; 2. they can disperse and become solitary breeding females or solitary roaming males; or 3. they can become the breeders of a group (Schradin *et al.* 2012).

During the breeding season, which in the Succulent Karoo typically lasts from August to November (Schradin and Pillay 2005), mice are group-living when population density is high. Groups usually consists of one to four closely related breeding females, one breeding male, and their adult offspring of both sexes, which remain natally philopatric and act as helpers at the nest (Schradin and Pillay 2004; Schradin *et al.* 2010a). Mice belonging to one group typically share a nest and a territory, but forage alone (Schradin 2004; Schradin and Pillay 2004). Striped mice are territorial and, while they are highly amicable with individuals belonging to their own group, they are aggressive towards intruders (Schradin 2004). Timing of sexual maturity, as well as dispersal age (and thus decision to adopt a certain tactic) depends on population density and territory availability (Schradin 2005; Schradin *et al.* 2010a). While striped mice are group-living when population density is high, they become solitary under conditions of low population density during the breeding season (Schradin 2005; Schradin *et al.* 2010a). Regardless of population density, however, striped mice always are group-living during the non-breeding season (Schradin *et al.* 2010a).

The socially flexible striped mouse represents an ideal species to investigate the reason for solitary-living and to understand how and why solitary and group-living individuals differ in their ecology, behaviours and physiology, as we can compare between the two different social tactics (solitary or group-living) by using a single

species, and we can thus eliminate the bias emerging from comparisons between different species.

3. AIMS OF THE STUDY

Careful experimental testing of concepts previously described through correlative and observational studies is important to clarify the role of factors affecting social organization and demonstrate causation. In the thesis hereby presented I aimed to experimentally test directly in the field the factors promoting solitary and group-living using a wild population of African striped mice. The thesis aims to answer the following questions:

(a) Does high population density favour group-living and reproductive competition favour solitary-living?

Under different population densities, striped mice can be either solitary or form complex family groups. Previous correlative studies indicated that intra-group conflict during the breeding season acts against group-living, while high population density and absence of reproductive competition after the breeding season favour group-living in striped mice (Schradin *et al.* 2010a). Here, I aimed to test experimentally whether high population density promotes group-living, while reproductive competition leads to dispersal and solitary-living. Using a field experiment, I manipulated the density of a population of striped mice by removing neighbouring groups and providing vacant territories for the remaining mice to move into, thus testing "the ecological constraints hypothesis". To avoid spatio-temporal bias, I carried out the experiment simultaneously using striped mice belonging to a single population, which were thus under identical ecological conditions. Taking advantage of the fact that striped mice are seasonal breeders (Schradin 2005), I tested for the role of reproductive competition by repeating the experiment in the non-breeding season. I predicted striped mice belonging to experimental groups to disperse and become solitary when population density decreased and reproductive competition was present during the breeding-season. I expected greater natal dispersal and decreased group sizes to occur in experimental groups than in control groups. Further, I predicted striped mice to

remain group-living in the non-breeding season when reproductive competition was absent even when vacant territories were available.

(b) Do solitary and group-living individuals differ in their social behaviour?

To understand the evolution of social behaviour it is important to study interspecific variation in social organization. Solitary and group-living species differ in many aspects of their ecology and life-histories, which are believed to arise as a consequence of differences in their social behaviours (Blumstein and Armitage 1998; Lacey 2000). To comprehend how social organisation influences social behaviour (or whether it is vice versa), it would be important to investigate whether the differences observed between solitary and group-living individuals are caused by environmental differences (especially differences in the social environment) or whether there are internal motivational differences between individuals that causes differences in their social behaviour. While there are good indications that dispersing individuals differ behaviourally from non-dispersing individuals, particularly in their social behaviours (Koolhaas *et al.* 1999; Sih *et al.* 2004; Rodriguez-Prieto *et al.* 2011), not much is known about the extent to which solitary individuals differ behaviourally from group-living ones within the same species. In the present thesis I studied whether the change from group- to solitary-living is associated with changes in social behaviour. Through a series of dyadic encounter in a neutral presentation arena, I compared the social behaviour of individuals that remained group-living with the social behaviour of individuals that dispersed and became solitary. Behavioural tests were performed on group-living and solitary individuals both before and after the latter dispersed, so that I could study whether group-living individuals that would later become solitary already showed behavioural traits that would lead to their dispersal, or whether they would change their behaviour only after adopting a new social tactic. The tendency of an individual to disperse has been linked with specific behavioural traits, such as aggression, exploration and sociability (Clark and Ehlinger 1987; Sih *et al.* 2004; Bell 2007). For example, it has been shown that the most asocial individuals tend to be the ones dispersing further from the natal nest (Cote *et al.* 2010). Thus I predicted individuals that would disperse and become solitary to be more aggressive, less amicable and more investigative than individuals remaining group-living.

(c) Do group-living and solitary individuals differ in their hormone profiles?

While the evolutionary reasons of group-living are well studied, the physiological mechanisms underlying different forms of social tactics are, in comparison, still poorly understood. Most of the endocrinological research on sociality has so far focused on comparing dominants and subordinates within the same group (Poiani and Fletcher 1994; Carlson *et al.* 2004; Malueg *et al.* 2009). However, to understand the proximate mechanisms that cause individuals to choose alternative forms of social tactics, we also need to know how solitary individuals differ from group-living ones. By studying group-living and solitary individuals of the same species we can determine hormonal correlates of sociality without the problem of confounding phylogenetic factors. In socially flexible species both males and females are able to change their social and reproductive tactic in response to changing environmental conditions and the endocrine system is expected to modulate such response (Lott 1991; Schradin *et al.* 2012). Studies of species with alternative reproductive tactics have shown that individuals following different tactics differ in their steroids levels (Oliveira *et al.* 2008). To determine whether differences in social organization correlated with hormonal differences, I collected blood samples from solitary and group-living individuals before and after the dispersal event. I predicted group-living striped mice to show higher corticosterone but lower testosterone levels compared to solitary-living individuals as a consequence of reproductive suppression or social stress resulting from life within the natal group.

(d) How does the availability of resources and population density affect space use patterns in African striped mice?

Most individuals frequently use the same area (Börger *et al.* 2006), thus traditionally the use of space by an individual has been studied using the home range concept (Waser and Jones 1983; McLoughlin and Ferguson 2000; Cagnacci *et al.* 2010), where a home range is defined as the area inhabited by an individual over a given time, which contains the necessary resources for its survival (Burt 1943). Several factors may be responsible for variation in home range parameters (Ostfeld 1990; Priotto *et al.* 2002; Hoset *et al.* 2008), however, ultimately, individuals are limited by the availability of resource and by the number of other individuals they need to

compete against to secure access to said resources (Lopez-Sepulcre and Kokko 2005; Schradin *et al.* 2010b). Several observational and some experimental studies have addressed the role that resources availability and population density play on home range sizes and overlap, yet none so far has been able to explain exhaustively whether these two factors together or one alone are responsible for home range variability. As home range can correlate with both population density and availability of food resources, it is important to address their effects in such a way where we can separate the effect of one factor from the other. Using two separate field manipulation experiments, I tested whether population density and the availability of food resources affect home range size and overlap in female African striped mice. I predicted females' home range sizes and overlap to be negatively affected by the provisioning of additional food and to be positively affected by the removal of neighbouring individuals.

4. THESIS OUTLINE

The thesis follows an integrative approach to study the reasons for solitary-living by incorporating ecological, physiological and behavioural aspects.

In **chapter 1**, I investigated the environmental causes that lead philopatrics individuals to either remain group-living or to disperse and become solitary. To do so, I investigated the influence of population density (as a proxy of ecological constraints) by removing groups of striped mice from the field and thus providing vacant territories for other striped mice to move into. I investigated the role of reproductive competition by replicating my experiments over several breeding and non-breeding seasons and comparing results obtained during these two periods. During the breeding season, when population density was low, more striped mice from groups directly neighbouring the removed groups moved into the vacant territories and became solitary than striped mice from control groups not neighbouring removed groups. However, during the non-breeding season individuals remained group-living despite the provisioning of free territories. My results support the ecological constraints hypothesis and show that reproductive competition can explain solitary-living.

In **chapter 2**, I investigated the differences in behavioural traits displayed by individuals following either a social or a solitary tactic. Because I was interested in the social behaviour of striped mice, I focused on behaviours important within the social contest (i.e. aggression, social investigation and amicability). As such behaviours often individually constant, representing what has been referred to as animal personalities (Reale *et al.* 2007; Stamps and Groothuis 2010) and correlate with each other, I looked at the existence of personalities and behavioural syndromes related to the specific social tactic adopted. Solitary striped showed higher levels of aggression and social investigation than their conspecifics that remained group-living, differences that were already present before individuals dispersed and changed from a social to a solitary tactic. The behaviour of dispersing mice was consistently different from the behaviour of mice that remained group-living, suggesting that only mice with a certain type of personality (e.g. more aggressive) might be predisposed to disperse and become solitary. While personality is important in facilitating dispersal and settlement in a new area, it seems that ultimately is the environment that provides the ideal conditions that facilitate individuals with more suitable personalities to switch their social tactics.

In **chapter 3**, I looked at the physiological consequences of adopting a solitary or a group-living tactic. To do so, I compared the corticosterone and testosterone levels in individuals following the two different social tactics. This chapter focused on understanding whether hormonal changes occur before behavioural changes and might thus cause them, or whether hormonal changes occur as a response to behavioural changes, that lead to changes in the (social) environment of an individual. Solitary striped mice of both sexes had significantly lower corticosterone levels than group-living individuals and solitary males had significantly higher testosterone levels than group-living individuals, indicating that solitary-living reduces physiological stress and ends reproductive suppression in both sexes. Adopting a solitary tactic might be seen as a way for a young adult that has reached reproductive maturity to escape reproductive suppression.

In **chapter 4**, I used two separate field manipulation experiments to test whether population density and the availability of food resources affect the spatial behaviour of striped mice. In a first experiment, which was conducted by Gaby Schmohl, an MSc student from the University of Zurich, we manipulated food availability by

providing supplemental food, thus testing for the effect of resource availability on home range patterns. In a second experiment I manipulated population density by removing groups of mice from the field and tested for the role of population density on home range patterns. I chose to focus my attention specifically on adult breeding females to limit bias emerging from potential age- and sex-dependent density effects. The number and the sex of neighbouring individuals were found to be important in regulating home range patters with neighbouring females having a particularly negative effect. Home range sizes of female striped mice showed a 20% decrease when food was provided and a 40% increase when neighbours were removed, thus indicating that population density might be the ultimate limiting factor in this species.

Overall, by using an experimental approach the study presented in this thesis aims to demonstrate causation for results of previous studies based mostly on correlative observational data. My research aims to further our understanding of the physiological mechanisms and the environmental factors that are responsible for the variation in social organization observed in nature.

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CHAPTER 1

Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*)

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Better off alone! Reproductive competition and ecological constraints determine sociality in the African striped mouse (*Rhabdomys pumilio*)

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Summary

1. While the reasons for group-living have been studied for decades, little is known about why individuals become solitary.

2. Several previous experimental studies could demonstrate that group-living can arises as a consequence of ecological constraints.

3. It has been argued that reproductive competition between group members leads to significant costs of group-living, being a main reason of solitary-living. However, so far, no studies tested experimentally whether reproductive competition can explain solitary-living.

4. Using a socially flexible species, the African striped mouse (*Rhabdomys pumilio*), we tested experimentally in the field whether dispersal and solitary-living are more likely to occur when reproductive competition is present.

5. We investigated ecological constraints, here expressed as a function of population density, by removing groups of striped mice and creating vacant territories. To control for the effect of reproductive competition, which occurs only during the breeding season, we performed experiments during both the breeding and the non-breeding season. This is the first removal experiment performed in a species with communal breeding during the non-breeding season.

6. During the breeding season, when population density was low, more striped mice from experimental groups moved into the vacant territories and became solitary than

striped mice from control groups. This is in support of the ecological constraints hypothesis.

7. During the non-breeding season, striped mice remained group-living despite the availability of free territories. Significantly, more striped mice became solitary-living during the breeding than during the non-breeding season. This is the first experimental support for the reproductive competition hypothesis explaining solitary-living.

8. Analysis of the sexual maturity of males showed that males, which became solitary had a higher reproductive potential than males that remained group-living. Analysis of the body mass data of females showed that more solitary females reproduced than group-living females. These results indicate that by becoming solitary individuals of both sexes avoided costs of reproductive competition within groups.

9. Our study provides experimental evidence that reproductive competition within groups can lead to dispersal and solitary-living.

Key-words: dispersal, population density, seasonality, social flexibility, solitary-living

1. INTRODUCTION

Animals display highly diverse social systems, ranging from solitary species to species that form complex societies, such as cooperative breeders with helpers at the nest (Taborsky 1994) and eusocial species (Burda *et al.* 2000). Much research has aimed to understand why social groups form and how they are maintained (Hamilton 1964; Wilson 2000). In contrast, no experimental study thus far has investigated the reasons for solitary-living, which is often simply regarded as the default mode of social organization. However, to understand the evolution of social organization, we also need to know why many individuals prefer a solitary life.

Social groups can form through the delayed dispersal of offspring. Such groups normally consist of dominant breeders and subordinate non-breeding offspring, which may act as helpers at the nest and gain indirect fitness benefits (Hamilton 1964; Emlen 1997). Remaining as subordinates within a social group can be costly for both sexes because of intra-group conflict, reproductive suppression and infanticide (Emlen 1982b; Brant *et al.* 1998). Thus, reproductive competition has been invoked as the main factor promoting dispersal and solitary-living in such groups (Emlen 1982a,b). Young adult individuals that delay dispersal and remain as philopatric subordinates in their natal group may incur costs: (i) by delaying onset of own reproduction; and (ii) by having to 'pay to stay' (Gaston 1978) by performing costly helping behaviour (MacColl and Hatchwell 2002; but see also Ekman *et al.* 1994; Vangen *et al.* 2001; Chapple 2003) for offspring that delay dispersal but do not help. Therefore, why would an individual delay dispersal to remain at home range?

Ecological constraints models (such as the 'habitat saturation hypothesis', Emlen 1982a) predict that offspring will remain philopatric when resources such as free territories or mating opportunities are scarce (Selander 1964; Pruett-Jones and Lewis 1990). Under such conditions, ecological constraints (e.g. high population density, Koenig *et al.* 1992) impose high costs on dispersal and individuals are thought to be doing 'the best of a bad job' by remaining philopatric. In other words, high dispersal costs imposed by ecological constraints increase the overall benefits of philopatry (Emlen 1982b, 1994; Stacey and Ligon 1991). Thus, the natal territory might become a 'safe haven' (Kokko and Ekman 2002) where young adult individuals have a better chance of survival by benefitting, for example, from group augmentation (Griesser *et*

al. 2006), as well as a place where they can acquire new skills, such as parental care (Lancaster 1971; Komdeur 1996). For example, under conditions of high population density, it might pay for a young individual to delay dispersal until it is better able to compete with others for limited resources such as breeding territories (Arnold and Owens 1998).

Several removal experiments in the field have shown that the removal of ecological constraints, such as high population density, can lead to dispersal, supporting the ecological constraints hypothesis and explaining group-living (Pruett-Jones and Lewis 1990; Jacquot and Solomon 2004). For example, Komdeur (1992, 1994) showed through a manipulation experiment that habitat saturation and territory quality were important in maintaining group-living in the Seychelles warblers (*Acrocephalus sechellensis*). By experimentally providing vacant breeding sites, Bergmüller et al. (2005) also demonstrated that helpers of a group-living cichlid (*Neolamprologus pulcher*) remained group-living in the presence of ecological constraints, but left and started independent breeding when ecological constraints were removed. Further experimental evidence was provided by Lucia *et al.* (2008), who manipulated population density in prairie voles (*Microtus ochrogaster*) and demonstrated that high population density leads to delayed dispersal and group formation. However, these experiments did not explain why individuals dispersed after ecological constraints were relaxed, although it has been long argued that costs associated with reproductive competition might promote dispersal and solitary-living (Emlen 1982a). However, it is more difficult to experimentally manipulate reproductive competition than ecological constraints. One way to investigate the effect of reproductive competition on dispersal decisions and sociality would be to compare dispersal between periods with and without reproductive competition, which could be achieved by using a seasonally breeding species with year round territoriality.

The African striped mouse (*Rhabdomys pumilio*) represents an ideal model organism to experimentally test whether ecological constraints favour group-living while reproductive competition favours solitary-living. Striped mice are socially flexible which means that individuals can switch between a group-living and a solitary tactic (Schradin *et al.* 2012). As a result, the social organization of a striped mouse population can range from solitarily to complex family groups consisting of one breeding male, several breeding females and their adult offspring of both sexes, which

remain philopatric as helpers at the nest (Schradin and Pillay 2004; Schradin *et al.* 2010a). Previous correlative studies have shown that striped mice are solitary-living during the breeding season if population density is low, whereas they remain group-living when population density is high (Schradin *et al.* 2010a). During the non-breeding season, when reproductive competition is absent, striped mice were found to be group-living independent of population density (Schradin *et al.* 2010a). These conclusions were based on correlative observational data and need experimental testing to control for other environmental factors. In our study, we aimed to test experimentally whether high population density promotes group-living and reproductive competition promotes dispersal. We manipulated population density by removing neighbouring groups of mice and providing vacant territories for other individuals to move into, thus testing 'the ecological constraints hypothesis', comparing between striped mice from control and experimental groups in the same population, at the same time, and thus under identical ecological conditions. In addition, by taking advantage of the fact that striped mice are seasonal breeders (Schradin 2005), we were also able to investigate the role that reproductive competition plays on sociality by performing removal experiments both in the breeding and in the non-breeding season. This is thus the first removal study on a communally breeding species, which was performed during the non-breeding season. We predicted greater natal dispersal and decreased group sizes in experimental groups than in control groups. Further, we expected striped mice to remain group-living during the non-breeding season when reproductive competition is absent, but to disperse and become solitary in the breeding season when reproductive competition is present.

2. MATERIAL AND METHODS

(a) Study area and study species

The study was conducted between August 2007 and August 2010 on a field site of 30 hectares located on the farm Klein Goegap (29º42.30' S–18º02.95' E) in the Northern Cape of South Africa. The vegetation type is classified as Succulent Karoo (Cowling *et al.* 1999), a semi-desert characterized by dwarf succulent shrubs. Here, striped mice typically form groups consisting of one breeding male and up to four breeding

females, which are born during the previous breeding season (Schradin and Pillay 2004). Their offspring remain philopatric long after reaching adulthood (at an age of approximately four to six; Schradin *et al.* 2009b), acting as non-breeding helpers in their natal group (Schradin and Pillay 2004). In this study, we refer to individuals born during the previous breeding season as 'breeders', and to individuals born in the season during which the experiments took place as 'philopatrics' (to avoid confusion over the term 'adult' as individuals belonging to both categories could have been classified as sexually mature adults). Under low population density, philopatrics can leave their natal group when 4–6 weeks old to start independent breeding. The breeding season typically lasts for about 4 months and coincides with the flowering of the nutritious ephemerals in spring (from August ⁄ September to November; Schradin and Pillay 2005a). The non-breeding season normally lasts for 9 months and takes place from the hot dry summer (December to April) to the end of the moist cold winter (from May to August).

(b) Determination of social tactic

All the striped mice within the study area were identified and their group affiliation determined using a combination of trapping, radio-tracking and behavioural observations (Fig. 1). Individuals were trapped directly at their nests using traps similar to Sherman's traps (26 x 9 x 9 cm). Each mouse was weighed, sexed, marked with permanent individual ear tags (National Band and Tag Co., Newport, KY, U.S.A.), and with a code-specific non-toxic hair dye (Inecto Rapido, Pinetown, South Africa). Markings were allowed for easy recognition of individuals during behavioural observations at their nests. Observations were conducted to determine group composition during the peak activity time for striped mice (i.e. in the early morning and in the late afternoon). All adult breeders and four philopatrics (two females and two males) of each group were fitted with radio-collars (Holohil, Carp, ON, Canada; 1.2–4.5 g). In total, we radio-tracked 126 males and 166 females during four breeding seasons, and 81 males and 93 females during four non-breeding seasons. Striped mice were radio-tracked using AOR 8000 radio-receivers (AOR USA Inc., Torrance, CA, USA) to determine home ranges and at night to determine composition of sleeping groups.

Striped mice were regarded as group-living if they shared the nest at night with the same individuals for at least 75% of the nights they were radio-tracked. Individuals that were found to spend at least 75% of the nights alone were regarded as solitary. We did not find any individuals falling in between these two percentages, i.e. no individual was recorded to spend between 26% and 74% of the nights with a group or alone.

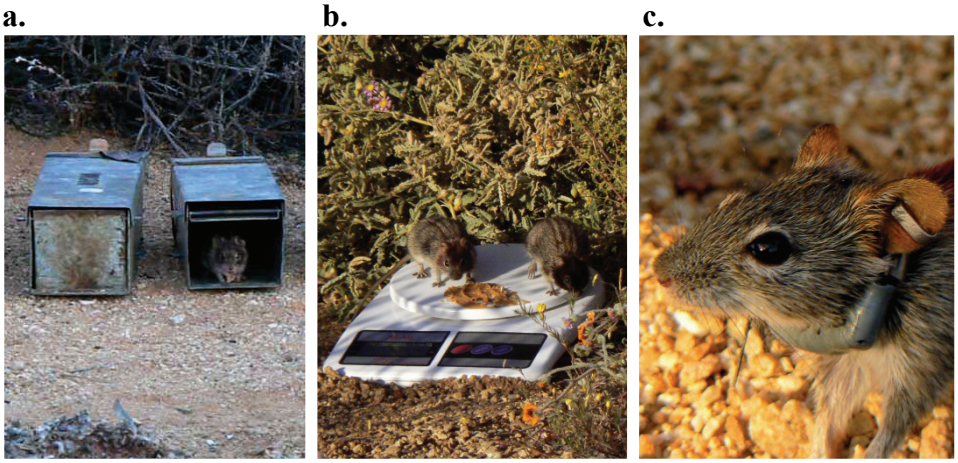

Figure 1.
An example of the techniques used in the field to determine striped mice social tactics. Figure 1.a. shows how mice were trapped (please note that the entrance of the trap pointed towards the nest and not away from it); figure 1.b. shows how mice were observed in front of their natal nest; and figure 1.c. shows a mouse fitted with a radio-transmitter.

(c) Experimental design

Removal experiments consisted of a replicated 2 x 2 factorial design with treatment (control, removal) and season (breeding, non-breeding) as factors. Each season we conducted two replicates of controls and two replicates of treatments. Local population density was manipulated by removing mice to create vacant territories for neighbouring striped mice to move into. All the experiments were performed in a valley, with the removal groups being the closest to the valley walls, such that these groups had neighbours only on one side. At the time of the experiments, all the territories within the study areas were occupied by striped mice groups and no open space remained between the different territories (for more information on how group enlarge their home ranges see Schradin *et al.* 2010b). Two replicates, separated by groups not used in the experiment, were carried out at the same time. Six groups were

used in each replicate: two groups were removed; two groups were used as experimental groups and two groups were used as control groups (Fig. 2).

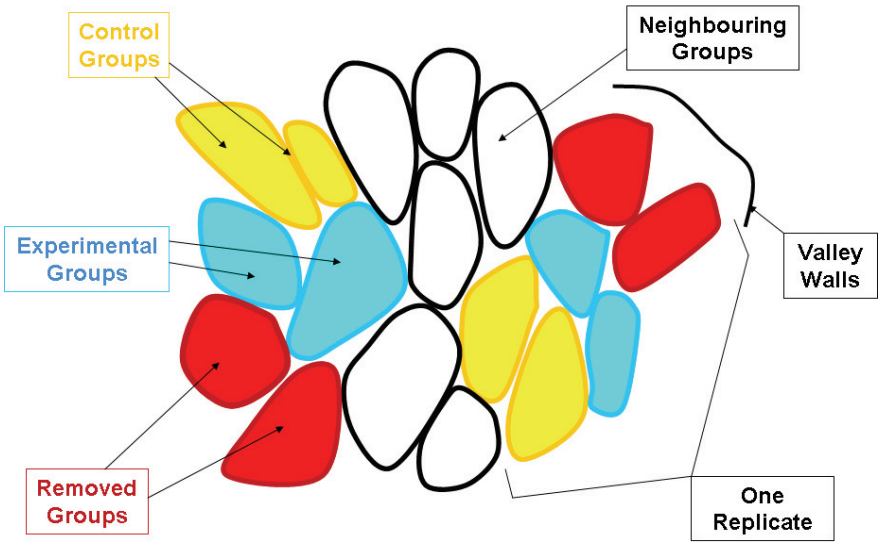

Figure 2.
Experimental design, with each polygon representing a group's home range. Each removal experiment consisted of two replicates of six groups each. Of these, two were removed (R1 and 2), two were monitored as experimental groups (E1 and 2) and two were used as control groups (C1 and 2). The white polygons separating the two replicates represent non-focal neighbouring groups, which were monitored only by trapping.

Experimental groups directly neighboured removed groups and control groups, whereas control groups only neighboured experimental groups and additional non-observed groups. In this way, striped mice from experimental groups directly experienced a local reduction in population density, while striped mice from control groups only experienced a reduction in population density when some of their neighbours from experimental groups dispersed into the newly available territories. Whereas each year different groups were used for experiments, within the same year the same groups were observed for both the breeding and the non-breeding season. Before removal, home range size and group affiliation were determined by radio-tracking mice six times per day for a period of 2 weeks (see Schradin and Pillay 2005b for details on the method used). Removal of groups took place immediately

after radio-tracking for home range had ended. Using a combination of trapping, radio-tracking and nest observation, we were able to establish with precision to which group each mouse belonged to, and we were thus able to successfully remove all the mice belonging to the 'removal groups'. Removed striped mice were used for breeding in a captive colony or in other studies (brain immunohistochemistry; unpublished data). Trapping was continued in the vacant territories and if striped mice of unknown origin (three individuals of 16 replicates) immigrated into the area, they were removed.

Striped mice from experimental and control groups were radio-tracked for an additional 4 weeks after removal, which from our experience is a time long enough to allow dispersal in this species (i.e. individuals will take between one and 3 weeks to disperse at the beginning of the breeding season, unpublished data). In total, eight replicates were carried out during the breeding season and eight replicates during the non-breeding season.

Local population density was measured separately for each replicate after removal of striped mice. For striped mice from experimental groups, local population density was calculated as the total number of individuals of control and experimental groups divided by the area occupied by removal, experimental and control groups. For striped mice from control groups, local population density was calculated as the total number of individuals of control and experimental groups divided by the area occupied by experimental and control groups. As local population density was influenced by group size of the studied control and experimental groups (local population density embeds group size), we did not include group size as a separate variable.

Males were regarded as potentially reproductively active when they were scrotal (i.e. their testes were fully descended; see Schradin and Pillay 2005a). Females were regarded as potentially reproductively active when they had a perforated vagina or showed signs of lactation (Schradin and Pillay 2005a). Parturition was determined by changes in females' body mass over a short period: a loss of >10 g indicated that a female gave birth (Schubert *et al.* 2009). A female was considered reproductively successful when she had given birth to at least one litter.

(d) Data analysis and statistics

Data analysis was performed using the statistical software R (version 2.11.0; R Development Core Team 2006, Vienna, Austria). All statistical tests were two-tailed. Data were tested for normality using the Shapiro–Wilk Normality test and are presented as mean ± SD. To test the predictions that relaxed ecological constraints and the presence of reproductive competition would lead to greater natal dispersal and solitary-living, we first used a Wilcoxon sign-rank test (with exact *p*-value calculations in R to correct for the small sample size). When the standard deviation was zero, we used the sign test instead. We used a generalized linear model (GLM) with a binomial error family to analyse the proportion of group-living striped mice (N = 32; 16 experiments and 16 controls during both seasons), including relative population density, season (breeding and non-breeding) and treatment (experiment and control) as factors. Lines of best fit were fitted to the data for the breeding and the non-breeding season. We also used a GLM with a poisson error family to test for significant differences in the likelihood of individuals from four different social classes to become solitary: breeding males, breeding females, philopatric males and philopatric females. We first fitted a saturated model with a three-way interaction between dispersal (group and solitary), reproductive status (breeder and philopatric) and gender (male and female). We then tested for the significance of this interaction by deleting it from a second model and comparing between the two models. Fisher's exact tests were used to compare: (i) the number of reproductively mature philopatric and solitary females at time of dispersal; (ii) the number of reproductively successful solitary and philopatric females at the end of the breeding season; and (iii) the number of males that became scrotal among solitary and philopatric males before and after dispersal took place.

3. RESULTS

During the breeding season and before removal, group size was 9.75 ± 3.45 individuals for control groups and 10.3 ± 5.34 individuals for experimental groups. During the non-breeding season and before removal, group size was 7.9 ± 2.99 individuals for control and 8.5 ± 2.94 individuals for experimental groups. Local population density was 11.10 ± 6.75 individuals/hectare for control groups and 12.71

± 6.63 individuals / hectare for experimental groups during the breeding season, and 8.67 ± 7.29 individuals / hectare for control and 7.56 ± 4.06 individuals / hectare for experimental groups during the non-breeding season.

During the breeding season, more striped mice from experimental groups became solitary (18.81 ± 13.08%) than striped mice from control groups (3.49 ± 7.59%; Wilcoxon sign-rank test, V = 0, N = 8; p = 0.008; Fig. 3). During the non-breeding season, nearly all striped mice remained group-living (experimental groups: 99.31 ± 1.96%; control groups: 100 ± 0%; sign test, V = 1, N = 8, p > 0.70; Fig. 3). Significantly, more striped mice from experimental groups dispersed and became solitary in the breeding (18.81 ± 13.08%) than in the non-breeding season (0.69 ± 1.96%; Wilcoxon sign-rank test; V = 35, N = 8; p = 0.016; Fig. 3).

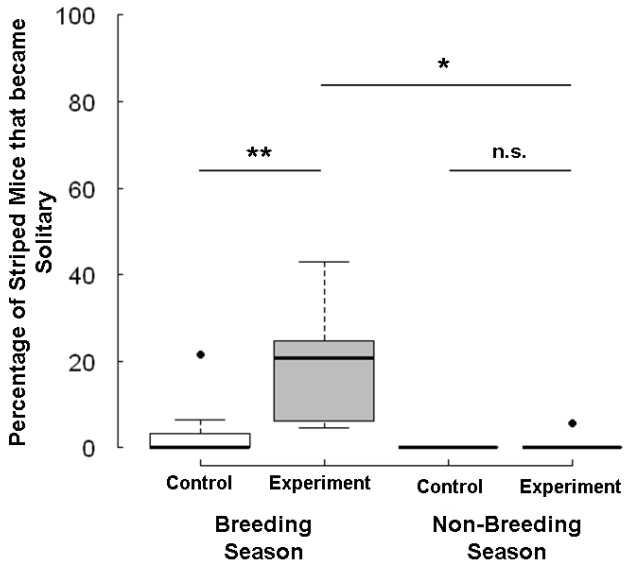

Figure 3.
During the breeding season, more mice from experimental groups became solitary than mice from control groups. During the non-breeding season, mice from experimental and control groups did not differ in their likelihood of becoming solitary. Mice were more likely to become solitary in the breeding season (time with reproductive competition) than during the non-breeding season. (*p < 0.05, ** < 0.01, n.s. = not significant).

For all 32 replicates combined (experimental and control groups during both seasons), the proportion of group-living striped mice was significantly influenced by season

(i.e. more mice became solitary during the breeding season: GLM: $F_{1,29} = 50.32$, $p < 0.001$), treatment (i.e. more mice from experimental groups became solitary: GLM: $F_{1,28} = 46.13$, $p < 0.001$) and by the interaction between season and local population density (population density played a role only during the breeding season but not during the non-breeding season; GLM: $F_{1,27} = 7.91$, $p = 0.009$), while local population density alone did not have an effect (GLM: $F_{1,30} = 1.21$, $p = 0.28$). The best fit for the relationship between population density (PD) and percentage of group-living striped mice (%GL) during the breeding season for the experimental groups (N = 8) was obtained from a hyperbolic curve ($R = 0.87$, $F_{2,7} = 574.01$, $p < 0.001$, Fig. 4), resulting in $y = a + (b/x)$, with y = %GL; a = 107.65; b = 274.65 and x = PD (Fig. 4).

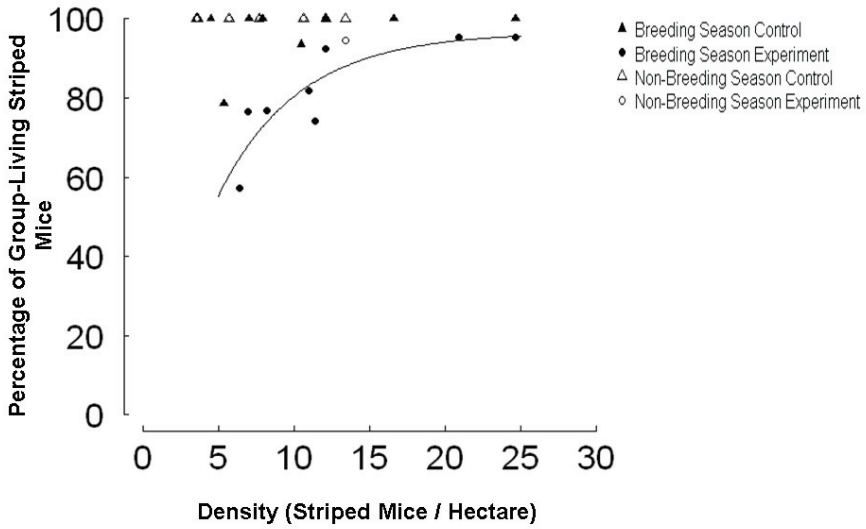

Figure 4.
Hyperbolic regression curve of the relationship between population density and group-living striped mice of experimental groups during the breeding season (black circles, black line, N = 8; $p < 0.001$). The hyperbolic regression curve was only fitted to the data of experimental groups during the breeding season (i.e. the black line only runs through the black dots). Data for experimental groups during the non-breeding season (white circles) and for control groups during the breeding (black triangles) and the non-breeding season (white triangles) were not significant. During the non-breeding season, many data overlap, thus not all the 16 points are clearly visible.

Breeding males (three of 28), breeding females (three of 27), philopatric males (19 of 76) and philopatric females (12 of 86) did not differ in their likelihood of becoming

solitary (i.e. there were similar sex-by-reproductive status interactions, GLM: Df Residuals = 0.62, $p = 0.43$).

At the time of dispersal, more females that would become solitary were reproductively mature (11 of 12 females) than females that remained philopatric (48 of 103 females; Fisher exact test, $p < 0.000$, Fig. 5). No females reproduced before dispersal. At the end of the breeding season, we found that more females that had become solitary had produced at least one litter (nine of 12 females), while very few females that remained philopatric had reproduced (13 of 103 females; Fisher exact test, $p = 0.004$, Fig. 6).

Figure 5.
At time of dispersal, significantly more females that became solitary were reproductively mature than females that philopatric (***$p < 0.001$).

Figure 6.
Significantly more solitary females reproduced during the breeding season than philopatric females (**$p < 0.01$).

At the time of dispersal, more males that would become solitary were scrotal (19 of 19 males) than males that remained philopatric (32 of 109 males; Fisher exact test, $p < 0.000$, Fig. 7). At the end of the breeding season, more solitary males (19 of 19) were scrotal than philopatric males (36 of 109; Fisher exact test, $p < 0.000$, Fig. 7). Philopatric males did not differ in scrotality at dispersal and at the end of the breeding season (Fisher exact test, $p = 0.66$, Fig. 7).

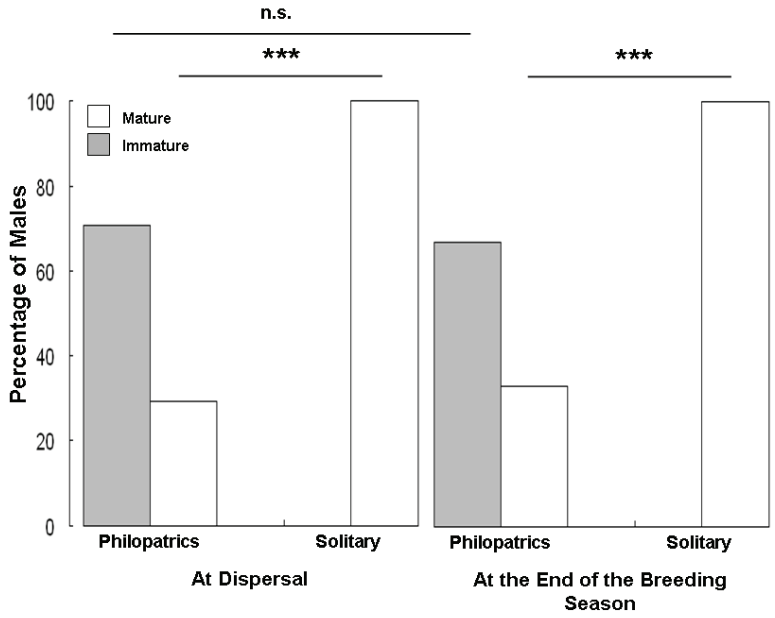

Figure 7.
Percentage of males that were scrotal with fully descended tests and thus regarded as sexually mature. Left: at the time of dispersal, a significantly higher percentage of solitary males was scrotal than philopatric males (***$p <$ 0.001). Right: at the end of the breeding season, a significantly higher percentage of solitary males was scrotal than philopatric males (***$p < 0.001$). Philopatric males were not more likely to be scrotal at the end of the breeding season than at dispersal ($p = 0.66$, not significant).

4. DISCUSSION

Striped mice became solitary and moved into the vacant territories as they became available, but only during the breeding season when reproductive competition was present. During the non-breeding season, striped mice remained group-living, even when vacant territories were available. Striped mice that became solitary had a higher reproductive capacity (males) or success (females), indicating that they were successful in avoiding reproductive competition. This is the first experimental field study providing evidence that reproductive competition can cause solitary-living when ecological constraints are relaxed.

Population density affected sociality in striped mice, but only during the breeding season. When population density was high and all the territories were occupied, striped mice remained group-living, supporting the habitat saturation hypothesis (Emlen 1982a; Hatchwell and Komdeur 2000). In contrast, more individuals dispersed

and became solitary when local population density was low and vacant territories were available, providing an important resource for striped mice (Schradin *et al.* 2010a). It has been suggested that not only the availability but also the quality of the resources available may affect the decision of an individual to disperse (Komdeur 1992). In our study, we did not measure territories quality; however, the territories from which we removed groups were directly adjacent the territories of experimental groups and were of similar size, supported a similar number of individuals as neighbouring experimental territories and striped mice belonging to experimental groups readily moved into the removed territories and took them over. This indicates that differences in territory quality did not play a significant role in our study. Our study thus indicates that breeding territories are a limiting resource for striped mice when population density is high.

The results of our study concur with correlative results obtained from an 8-year-long field study on a neighbouring population of striped mice, living only three kilometres away from our experimental field site (Schradin *et al.* 2010a). Similarly, to the observations of Schradin *et al.* (2010a), our experiment showed that population density influences sociality, but only during the breeding season. In both studies, it was found that a hyperbolic curve is the best fit for the relationship between population density and percentage of group-living striped mice during the breeding season, while outside the breeding season, no relationship exists between population density and sociality (compare our Fig. 3 with Fig. 2 in Schradin *et al.* 2010a). Previous experiments performed during the breeding season in fish (Bergmüller *et al.* 2005; Stiver *et al.* 2006; Wong 2010), birds (Pruett-Jones and Lewis 1990; Walters 1991; Komdeur 1992) and mammals (Jacquot and Solomon 2004) already confirmed predictions of the ecological constraints hypothesis especially that groups form when resources are limited (Koenig *et al.* 1992; Kokko and Ekman 2002; Baglione *et al.* 2005). Ours is the first experiment in a mammal under natural conditions (vs. experiments in enclosures: Jacquot and Solomon 2004; Lucia *et al.* 2008), demonstrating the importance of territory availability on sociality.

While ecological constraints could explain why striped mice remained natally philopatric when population density was high, they cannot explain why they did not disperse when vacant territories were available in the non-breeding season. Reproductive competition can be high in striped mice of both sexes. In each group, a

single breeding male monopolizes several communally breeding females (Schradin *et al.* 2009a) and reproductively suppresses the adult philopatric males of the group (Schradin *et al.* 2009b). Female striped mice show intra-sexual aggression and infanticide towards the pups of other females within the group (Schradin *et al.* 2010a). Thus, we attribute the difference in the results obtained between the breeding and non-breeding seasons to the role of reproductive competition, which only occurs during the breeding season.

If reproductive competition is the reason for becoming solitary-living in striped mice, then solitary striped mice should be reproductively more successful than group-living ones. In support of this, we found that solitary males were scrotal and thus fully sexually mature, while many philopatric males (of the same age and body mass as solitary males) were not scrotal. In several cooperative-breeding species, subordinates are reproductively suppressed by dominant breeders (Blumstein and Armitage 1999; Saltzman *et al.* 2006; for male striped mice see Schradin *et al.* 2009b) or may delay reproductive maturity to avoid aggressive expulsion by the dominant breeders (Hamilton 2004). In our study, most of the male striped mice that remained philopatric also remained unscrotal during the entire breeding season, suggesting that they were unable to escape reproductive suppression. While we could not measure reproductive success of males, our data indicate that solitary males, which were all scrotal, might have reproduced, while most of the philopatric males could not reproduce, as they were not scrotal. For females, our data gave even better support: females that dispersed were more reproductively mature than group-living philopatrics, and 75% of solitary females reproduced, but only 13% of philopatric females. Our results indicate that striped mice that became solitary reduced costs of reproductive competition within groups, which were significant for striped mice that remained philopatric.

While reproductive competition is one cost of group-living, remaining within the natal group may also offer considerable advantages. Benefits of group-living include enhanced protection against predation, better resource defence and energy savings (Krause and Ruxton 2002). Predation pressure, mainly from many-horned adders (*Bitis cornuta*), jackal buzzards (*Buteo rufofuscus*) and African wildcats (*Felis silvestris lybica*), was significant at our field site, with > 40% of radio-collared striped mice lost before the end of our experiment. Increased group vigilance has been

suggested as one of the potential advantages of communal nesting and has been reported for several species (Gagliardo and Guildford 1993; Krebs and Davies 1993). Striped mice sleeping in groups might benefit from increased vigilance against potential predators at night (Schradin 2005). Additionally, groups may be better able to defend territories than single individuals, as all group members participate in territorial defence (Schradin 2004). Territories contain essential feeding and nesting areas during periods of scarcity, such as during the dry season. Most importantly, by remaining within the group, striped mice can obtain thermoregulatory benefits from huddling together at night, significantly reducing energy expenditure and water consumption: benefits are particularly important for a species that lives in a semi-desert environment (Scantlebury *et al.* 2006). Costs of group-living can include intra-group competition for limited resources such as food, and transmission of parasites (Danchin *et al.* 2008). Significant benefits of group-living exist in striped mice, which are predicted to be higher than costs of group-living during the non-breeding season, leading to group-living. However, when the extra costs of reproductive competition arise during the breeding season, such as reproductive suppression and infanticide, the costs seem to be higher than the benefits, leading to solitary-living if costs of dispersal (= benefits of philopatry) are low.

Dispersal and resulting solitary-living of striped mice can thus be explained as a tactic to avoid reproductive competition and, in the case of young adult philopatrics, to start independent breeding. While most of the individuals that dispersed were young philopatrics, we also observed breeding adults born during the previous breeding season dispersing and becoming solitary, and there was no significant difference between breeders and philopatrics. Striped mice are socially flexible, i.e. individuals of both sexes can follow alternative reproductive tactics (Schradin *et al.* 2012). Male striped mice have the following tactics: (i) to remain as philopatric helpers in their natal group; (ii) to disperse and become solitary roamers with defined home range; or (iii) to become group-living territorial breeders (Schradin *et al.* 2009a). Female striped mice have the following options: (i) to remain as philopatric helpers in their natal group; (ii) to disperse and breed singly; or (iii) to breed communally (Schradin *et al.* 2010c). When population density is high, being a territorial breeding male is the most successful tactic, but when population density is low and resources, such as females, are not clumped (i.e. females breed solitarily and not communally), being a

roamer is the preferred tactic (Schradin and Lindholm 2011). Our results concur with previous correlative studies demonstrating that at the beginning of the breeding season, striped mice of both sexes that were born during the previous breeding season leave huddling groups and follow a solitary tactic, if vacant territories are available (Schradin *et al.* 2010a).

Whereas several previous experimental studies demonstrated the importance of ecological constraints in maintaining group-living (Jacquot and Solomon 2004; Dickinson and McGowan 2005; Griesser *et al.* 2008), no experimental studies thus far tested the reasons for solitary-living. This is peculiar as reproductive competition within groups has often been used as a plausible explanation for why individuals disperse and become solitary (Emlen 1982a, 1997). In our study, we were able to show that free-living striped mice leave communal groups and become solitary if vacant territories are provided experimentally, but they do so only during the breeding season. Population density alone could not explain this, and as our controls during the non-breeding season were performed during both the hot dry summer when food availability is low and the moist cold winter, when food availability is high, neither temperature nor food per se is likely to explain our results (see also Schradin *et al.* 2010a). Thus, the main difference between the breeding and the non-breeding season is the presence or absence of reproductive competition, which is the most parsimonious explanation for the differences in sociality we found. Further, we found evidence for both sexes that striped mice were able to avoid reproductive competition by becoming solitary. This is to our knowledge so far the best experimental evidence that reproductive competition within groups is responsible for dispersal and can lead to solitary-living.

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CHAPTER 2

Differences in social behaviour between group-living and solitary African striped mice, *Rhabdomys pumilio*

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Differences in social behaviour between group-living and solitary African striped mice, *Rhabdomys pumilio*

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Abstract

Little is known about the extent to which solitary individuals differ in their social behaviour from group-living ones within the same species. Using the socially flexible African striped mouse, we tested through a series of dyadic encounters in a neutral arena whether group-living mice that later became solitary differed from their philopatric conspecifics. We compared philopatric and solitary mice both before and after dispersal. We predicted striped mice that became solitary would be more aggressive, less amicable and more investigative than individuals that remained group-living, and would change their social behaviour after changing from group to solitary-living in the same direction (becoming more aggressive, etc.). Dyadic encounters were conducted on 42 group-living individuals and 13 individuals that were first group-living and later became solitary. Striped mice that became solitary showed higher levels of aggression and social investigation than their conspecifics that remained group-living, differences that were already present before individuals dispersed. Dispersing striped mice showed a negative correlation between amicability and aggression towards opposite-sex individuals, which could be linked to sexual motivation. A second behavioural syndrome in the form of a positive correlation between aggression and social investigation towards same-sex individuals might have indicated that dispersing striped mice were ready to defend their own territory. Our study provides evidence that within the same population and at the same time, individuals that disperse and become solitary differ behaviourally from their group-living conspecifics even before dispersal, and further change their behaviour after dispersal in an evolutionarily adaptive way.

Key-words: African striped mice, aggression, amicability, behavioural syndrome, dispersal, group-living, personality, *Rhabdomys pumilio,* social behaviour, solitary

1. INTRODUCTION

Animals display a great diversity of social organization, ranging from solitary species to species that form complex societies (Wilson 2000). Solitary and group-living species display distinct social organizations, which are believed to arise as a consequence of differences in social behaviours (Blumstein and Armitage 1998; Lacey 2000). Individuals of solitary species live alone and, apart from when mating, offspring rearing and defending their territory, rarely interact with conspecifics (Lacey and Wierczorek 2003). In contrast, individuals of group-living species remain together for prolonged periods of time, interacting frequently and extensively with one another to a much greater degree than with conspecifics of other groups (Wilson 2000), for example when sharing feeding and nesting sites (Blumstein and Armitage 1998; Solomon 2003). As a consequence, the variety of social behaviours displayed by group-living species exceeds that of solitary species. In addition, social bonding between adult individuals characterizes group-living birds and mammals, but is usually restricted to mother-offspring bonding in solitary species (Leckman *et al.* 2005). To understand the evolution of social behaviour it is important to study interspecific variation in social organization. However, social and solitary species differ in many aspects of ecology, life history traits; and behaviour; thus it is difficult to study a single factor (such as social behaviour) without the problem of confounding effects. To understand how sociality influences social behaviour it would therefore be advantageous to study the behaviour of individuals belonging to a single species that can be either solitary or group-living in the same environment.

Socially flexible species give us a unique opportunity to test the behavioural differences between solitary and group-living individuals within the same species and population. In species that have a socially flexible organization, both group- and solitary-living individuals can occur within the same population, at the same time and in the same environment (McGuire and Getz 1998; Schradin *et al.* 2012). In changing environmental conditions, individuals of socially flexible species are able to switch between alternative social tactics (Oliveira *et al.* 2008; Schradin *et al.* 2009a; Schradin *et al.* 2012). By using individuals of socially flexible species, we can thus investigate the behavioural differences between solitary and group-living individuals using a single species, which allows us to avoid confounding environmental and phylogenetic factors in interspecies comparisons. Offspring of socially flexible

species are typically raised in family groups and have the choice to remain group-living when reaching adulthood, for example becoming a philopatric helper, or to disperse and follow a solitary breeding tactic. An individual's dispersal from its natal site to a site where it may breed is one of its most important life history events (Bekoff 1977). The success of natal dispersal might depend on several factors, such as the availability and quality of resources (Emlen 1982; Pruett-Jones and Lewis 1990; Koenig *et al.* 1992), and the behavioural phenotype of the disperser (Hoset *et al.* 2011). Several studies have shown that dispersing individuals differ from non-dispersers in their behavioural traits (Svendsen 1974; Brandt 1992; Bowler and Benton 2005), particularly in their social behaviours (Koolhaas *et al.* 1999; Sih *et al.* 2004a; Rodriguez-Prieto *et al.* 2011). For example, studies of voles and lemmings have revealed dispersal to be linked with increased aggression, decreased sociability and increased exploration (Myers and Krebs 1971; Ims 1990; Hoset *et al.* 2011). Furthermore, reactive (i.e. individuals that have a conservation or withdrawal stress response) and less aggressive individuals tend to be more adaptable and show greater behavioural flexibility to new situations than proactive (i.e. individuals that have a fight or flight stress response) and more aggressive individuals (Koolhaas *et al.* 1999; Sih *et al.* 2004a). As a consequence, proactive individuals are thought to be more likely to disperse (Rodriguez-Prieto *et al.* 2011). While there are good indications that dispersing individuals differ behaviourally from non-dispersing individuals, not much is known about the extent to which solitary individuals differ behaviourally from group-living ones within the same species. If such differences exist, it would be important to know whether they are a consequence of the new environmental conditions experienced by dispersers or whether they occur independently of the dispersal event and they are thus a result of individuals' different personalities (Hoset *et al.* 2011).

Personality, defined as individual consistencies in behavioural traits (such as aggression, exploration and sociability) over time and across context, is a phenomenon observed in several species from unicellular organisms to higher vertebrates (Dall *et al.* 2004; Reale *et al.* 2007; Bell *et al.* 2009). Different personality traits are often correlated with each other, in behavioural syndromes (Clark and Ehlinger 1987; Sih *et al.* 2004b; Bell 2007). For example, aggressive individuals are often also bolder (Reale *et al.* 2007). Specific personalities, for example high

boldness, might underlie good dispersal abilities that lead to lower costs of dispersal and might facilitate settlement in a new environment compared to individuals with a different personality, for example very shy individuals (Clobert *et al.* 2009). Several studies have shown a link between dispersal tendencies and different behaviours, such as aggression, exploration and sociability, in what is known as a dispersal syndrome (Clark and Ehlinger 1987; Sih *et al.* 2004b; Bell 2007). Cote *et al.* (2010b) have shown the existence of a dispersal syndrome linked with sociability, with the most asocial individuals dispersing further away from the natal nest. Thus, studying the behaviour of individuals of socially flexible species before and after a switch from group to solitary-living can help us to understand whether individuals within the same species that live solitarily differ consistently in their social behaviour from group-living ones, indicating the existence of a dispersal syndrome.

The socially flexible African striped mouse (*Rhabdomys pumilio*) is one species that allows comparisons between group- and solitary-living individuals within the same population. In the Succulent Karoo of South Africa, striped mice normally form communally breeding groups consisting of one breeding male, two to four breeding females and their philopatric offspring (Schradin and Pillay 2004). However, if population density is low during the breeding season, philopatric mice leave their natal group, disperse and start solitary breeding; in doing so, they switch from group-living to solitary-living (Schradin *et al.* 2010a; Schoepf and Schradin 2012). We studied whether the change from group to solitary-living is associated with changes in social behaviour. In particular, we tested: (1) whether individuals that later become solitary differed in their behaviour from individuals that remained group-living before dispersal and whether these differences were present between solitary and dispersing individuals of the same litter; (2) whether individuals differed behaviourally before and after switching from group to solitary-living; (3) whether individuals that remained group-living differed behaviourally before and after other group members dispersed; (4) whether within each tactic (solitary and group-living individuals) behaviour remained consistent before and after dispersal, indicating personality; and (5) whether different behaviours (e.g. aggression, amicability and social investigation) would be correlated in different behavioural syndromes that would be specific to either group-living or solitary individuals. We predicted individuals that would disperse and become solitary would be more aggressive, less amicable and more

investigative than individuals staying in their natal group. Because group size, and thus within-group competition, declined after individuals dispersed, we tested whether individuals that remained in their natal group changed their behaviour after the dispersal of other group members. We predicted behavioural differences between group-living and solitary mice would already be present before dispersal, that is, that mice that would later disperse would already be less social before switching to solitary-living. Finally, we predicted behaviours would be consistently different between group-living and solitary individuals (i.e. solitary mice would be consistently more aggressive than group-living mice) and would be correlated in behavioural syndromes that would reflect the specific tactic adopted (i.e. aggression would be positively correlated with social investigation in solitary individuals but not in group-living individuals).

2. MATERIAL AND METHODS

(a) Study area and animals

Data were collected during the breeding season from August to November in 2007-2010, when dispersal typically occurs and striped mice might switch from group-living to solitary-living (Schradin *et al.* 2010a; Schoepf and Schradin 2012). The study was conducted on a field site located on the farm Klein Goegap (29º42.30' S–18º02.95' E) near the town of Springbok in South Africa. All the striped mice within the study area were identified and their social tactics (solitary or group-living) determined using a combination of trapping, radio-tracking and behavioural observations (Schradin *et al.* 2010a; Schoepf and Schradin 2012). Striped mice were trapped at their nest, sexed, weighed and marked permanently with ear tags (National Band and Tag Co., Newport, KY, U.S.A.). Additionally, each individual received a specific temporary mark, which was applied using a nontoxic hair dye (Inecto Rapido, Pinetown, South Africa) and allowed for easy individual recognition during behavioural observations. Trapping and marking methods were identical to those used by Schradin *et al.* (2010b). All adult breeders and four philopatric mice (two females and two males) of each studied group were fitted with radio-collars (Holohil, Carp, Ontario, Canada; 1.2 - 4.5 g; in total 126 males and 166 females). Radio-collars always weighed less than 8% of a mouse's body mass (mostly less than 5%), with the

lightest collars (1.2 g) fitted on the smallest juveniles (20 g). No individuals that weighed less than 20 g received a radio-collar and all radio-collars were removed after 10 weeks of radio-tracking. We did not find any indication that radio-collars caused increased mortality, and there is no indication that striped mice carrying radio-transmitters have increased stress hormone levels (Schradin 2008). Striped mice were radio-tracked to determine home range and composition of sleeping groups at night (Schradin and Pillay 2005a, 2006). Striped mice that shared the same nest at night on more than 75% of occasions were regarded as group-living whereas those that slept alone on more than 75% of occasions were regarded as solitary-living; no values occurred in between (i.e. there were no individuals that displayed intermediate scores; for more details see Schoepf and Schradin 2012). All striped mice used were from a field experiment in which we experimentally reduced population density by removing individuals from additional groups (not considered here), demonstrating that decreased population density induces dispersal and, in several mice, a switch from a group-living to a solitary-living tactic (Schoepf and Schradin 2012).

(b) Behavioural phenotyping

Striped mice are diurnal, with their peak activity periods in the early morning and late evening (Schradin and Pillay 2004). Striped mice were trapped in the early morning directly at their nests soon after they emerged. Each mouse was kept in its own trap and transported 3 km to our research station for testing. Once at the station, they were transferred to a Perspex cage (38 x 22 cm and 15 cm high) provided with bedding (straw), water (*ad libitum*) and food (five sunflower seeds). Mice were allowed to settle for 10 min in the test room. All tests were performed in a neutral arena made out of wood chip (80 x 65 cm and 94 cm high, with a partition in the middle, Fig. 1). Each stimulus and focal mouse was introduced to the arena and allowed to settle for 5 min before the partition was removed. The presentation arena was cleaned each time before a new encounter took place using diluted Dettol Antiseptic Liquid (Reckitt Benckiser Pharmaceuticals Ltd., Elandsfontein, South Africa) and water.

Figure 1.
The neutral presentation arena used for the behavioural phenotyping.

Each focal individual went sequentially through three successive tests: (1) pup encounter (5 min); (2) opposite-sex encounter (10 min); and (3) same-sex encounter (10 min). Stimuli mice (pup, opposite and same sex) were obtained from a captive colony, which is permanently maintained at the research station. All the pups used in the tests were less than 10 days old (i.e. pre-weaned), as striped mice cannot distinguish between their own and strange pups that are younger than 10 days old (Pillay 2000). Adult stimulus animals were always lighter than the focal animal, as body mass is known to have a positive influence on the outcome of aggressive encounters (Schradin 2004) and we wanted the focal mouse to initiate encounters. At the end of each test, mice were returned to their cages where they were allowed to rest for 5 min. A different stimulus mouse was used for each test. We recorded the behaviour of focal mice by direct observations. Three different categories of behaviour were scored: (1) amicable behaviours (i.e. grooming, huddling and licking); (2) social investigation (i.e. sniffing); and (3) aggression (i.e. chasing, standing upright for fighting and threat displays). The frequency of the behaviours was recorded using focal animal sampling (Martin and Bateson 1993). Most of the agonistic encounters observed involved chasing and threat displays. However, in a few cases (< 4% of all tests performed) encounters had to be interrupted because of high levels of aggression. Tests were immediately terminated as soon as (1) pups were

pushed and (2) older individuals started wrestling (before any biting could occur). In this way we ensured that none of the individuals used in the tests received any physical injuries. As we could not know beforehand which individual was going to become solitary, before dispersal we tested most of the philopatric individuals belonging to experimental groups (for more details see Schoepf and Schradin 2012). Behavioural tests were conducted on a total of 42 focal mice (females: N = 18; males: N = 24) before focal mice dispersed and became solitary. All focal mice were philopatric. Six focal mice that remained group-living (females: N = 2; males: N = 4) and 13 focal mice that became solitary (females: N = 7; males: N = 6) were tested a second time after dispersal and tactic change. All behavioural tests were carried out in the early morning. At the end of each test, captive mice were immediately returned to the captive colony. Captive mice were later used for other behavioural studies (not considered here). Wild mice were taken back to the field and released in the same spot where they had been captured once all three tests were performed. All mice (captive and wild) were returned in good condition. The study obtained ethical clearance from the University of the Witwatersrand (AESC: 2007 / 38 / 04).

(c) Data analysis

Data analysis was performed using the R statistical software version 2.11.0 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). Exact P value calculations were performed on all tests to correct for small sample sizes. We used a Mann-Whitney U test to test the prediction that individuals that would become solitary (N = 16) differed in their behavioural traits from individuals that remained group-living (N = 36). Paired Wilcoxon sign-rank tests were used to assess behavioural changes within the same individual, particularly the predictions that (1) a change in tactic from group-living to solitary would lead to changes in aggression, social investigation and amicability (solitary individuals before and after tactic change: N = 13), and (2) dispersal of group members would trigger a behavioural change in those individuals that remained at their nest (group-living before and after individuals dispersed: N = 6). We assessed the behavioural consistency of the traits by calculating Kendall's *W* coefficient of concordance. With this test we measured consistency in rank scores of behavioural traits among group-

living and solitary mice before and after dispersal (after Hoset *et al.* 2011). We checked for the existence of a behavioural syndrome by performing pair-wise Spearman rank correlations (r_S) between the different behavioural traits. P values of multiple comparisons tests for personalities and behavioural syndromes were adjusted using the Benjamini-Hochberg method (Benjamini and Hochberg 1995), which allowed us to control for both type I and II errors. Several factors such as body mass and sex have been shown to influence behavioural traits. For example, several studies on small mammals have found aggressive behaviour to be influenced by sex (Boonstra 1978; Ebensperger 1998; Andreassen and Gundersen 2006). Age, body weight and reproductive condition are known to have an effect on the tactic adopted in striped mice (Schradin *et al.* 2009a; Schoepf and Schradin 2012), and thus we used generalized linear mixed models (GLMM) fitted with a Poisson distribution to test for the effects of sociality (group-living or solitary), dispersal (before or after), sex, weight (g), type of individual presented (pup, opposite sex or same sex), age and reproductive status (mature or immature) on each behavioural trait as dependent variable (aggression, social investigation or amicability) and sociality (group-living or solitary). Individual identity was included in each model as a random factor as individuals were measured repeatedly in the three tests. Each GLMM was fitted by Laplace approximation and had a sample size of N = 252. Individual identity was defined as a random factor and we selected the best model by a stepwise backward procedure (following Crawley 2007). We used a linear mixed-effect model (LMM) to compare the behaviour of group-living versus solitary striped mice that were from the same communal litter (raised at the same time in the same group) before dispersal. Each LMM had one of the behaviours as the response variable; dispersal status (will disperse and will not disperse), sex and the type of individual presented were the fixed factors, and individual ID and Group were the random factors. Data for GLMM and LMM were tested for normality using the Shapiro-Wilk normality test. Data are presented as mean frequency/5 min ± SE.

3. RESULTS

(a) Behaviour of dispersing and non-dispersing mice before dispersal

Dispersing striped mice were significantly more aggressive towards same-sex individuals than non-dispersing mice (W = 48, $p < 0.001$; Fig. 2a), but not towards pups (W = 145.5, $p = 0.05$; Fig. 2a) nor towards opposite-sex individuals (W = 205, $p = 0.73$; Fig. 2a). Dispersing mice displayed significantly more social investigation than non-dispersing mice in all three trials: pup encounters (W = 62, $p < 0.001$; Fig. 2b), opposite-sex encounters (W = 102, $p = 0.01$; Fig. 2b) and same-sex encounters (W = 118, $p = 0.04$; Fig. 2b). Dispersing mice showed significantly more amicable behaviours than non-dispersing mice during opposite-sex encounters (W = 121.5, $p = 0.03$; Fig. 2c), but not during pup encounters (W = 193.5, $p = 0.95$; Fig. 2c) nor during same-sex encounters (W = 227, $p = 0.21$; Fig. 2c).

Mice raised in the same litter differed significantly in their aggression levels depending on whether they later dispersed or remained group-living (LMM: t = -2.26, $p = 0.04$) and on the sex of the stimulus mouse presented (dispersing striped mice were more aggressive towards same-sex individuals; t = 2.15, $p = 0.03$), but not the sex of the focal individual (t = -0.41, $p = 0.68$). Amicability and social exploration in individuals that were raised in the same litter were not significantly influenced by dispersal status (amicability: t = -0.63, $p = 0.53$; social exploration: t = -0.21, $p = 0.84$), sex (amicability: t = 0.87, $p = 0.39$; social exploration: t = 0.68, $p = 0.51$) or the type of individual presented (amicability: t = -1.69, $p = 0.09$; social exploration: t = 1.06, $p = 0.29$).

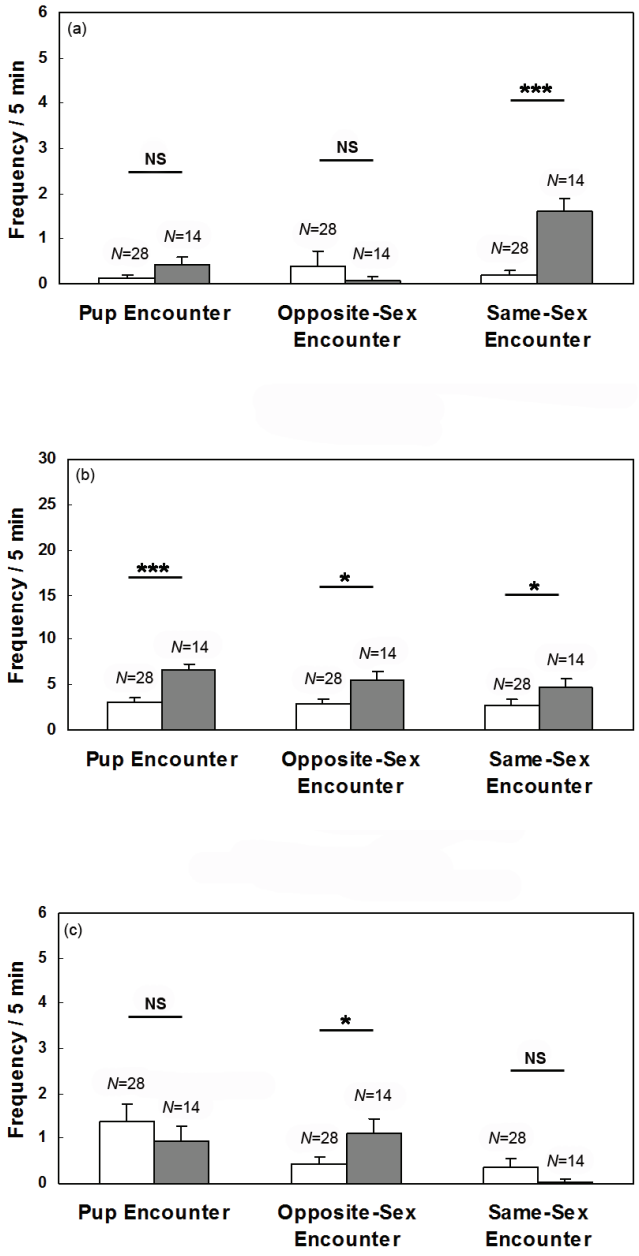

Figure 2.
Behavioural differences between striped mice that remained group-living (in white, N = 28) and that became solitary (in grey, N = 14), before dispersal took place. Striped mice were presented with pups, same-sex or opposite-sex individuals in a neutral test arena. (a) Aggression, (b) social investigation and (c) amicable behaviours. *$p < 0.05$; *** $p < 0.001$. Data are presented as mean frequency/5 min ± SE.

(b) Behavioural changes in mice that became solitary

After dispersal, striped mice showed significantly more aggressive behaviour towards pups (Wilcoxon sign-rank test: V = 21, N = 13, $p = 0.03$; Fig. 3a) and towards same-sex individuals (V = 78, N = 13, $p = 0.002$; Fig. 3a) than before dispersal. This was not the case for aggressive behaviour shown towards opposite-sex individuals (V = 10.5, N = 13, $p > 0.99$; Fig. 3a). After becoming solitary, striped mice showed significantly higher frequencies of social investigating behaviour in all three tests: pup encounter (V = 87.5, N = 13, $p = 0.004$; Fig. 3b), opposite-sex encounter (V = 90, N = 13, $p = 0.002$; Fig. 3b) and same-sex encounter (V = 91, N = 13, $p = 0.002$; Fig. 3b). Striped mice showed significantly more amicable behaviours towards members of the opposite sex after they became solitary (V = 65, N = 13, $p = 0.005$; Fig. 3c), but not towards mice of the same sex (V = 0, N = 13, $p = 0.35$; Fig. 3c) nor towards pups (V = 6, N = 13, $p = 0.19$; Fig. 3c).

(c) Behaviour of group-living mice after group member dispersal

Group-living individuals did not show any significant changes in aggressive behaviour towards pups (before dispersal of group members: 0.00 ± 0.00; after dispersal of group members: 0.76 ± 0.48; Wilcoxon sign-rank test: V = 6, N = 6, $p = 0.17$), towards members of the opposite sex (before dispersal of group members: 0.00 ± 0.00; after dispersal of group members: 0.33 ± 0.33; V = 1, N = 6, $p > 0.99$) and towards same-sex individuals (before dispersal of group members: 0.99 ± 0.45; after dispersal of group members: 1.50 ± 1.09; V = 7, N = 6, $p = 0.58$). Group-living individuals did not differ in their social investigation before and after dispersal of group members during pup encounters (before dispersal of group members: 1.50 ± 0.81; after dispersal of group members: 2.92 ± 0.93; V = 14, N = 6, $p = 0.10$), during opposite-sex encounters (before dispersal of group members: 4.83 ± 2.06; after dispersal of group members: 8.33 ± 2.97; V = 16, N = 6, $p = 0.29$) and during same-sex encounters (before dispersal of group members: 6.96 ± 3.57; after dispersal of group members: 8.48 ± 4.46; V = 10, N = 6, $p = 0.59$). Furthermore, we did not find any significant difference in amicable behaviours of group-living individuals before and after individuals dispersed for pup encounters (before dispersal of group members: 0.67 ± 0.49; after dispersal of group members: 0.17 ± 0.17; V = 0, N = 6, p

> 0.99); opposite-sex encounters (before dispersal of group members: 1.67 ± 1.05; after dispersal of group members: 1.50 ± 0.81; V = 3, N = 6, $p > 0.99$) and same-sex encounters (before dispersal of group members: 0.50 ± 0.67; after dispersal of group members: 1.00 ± 0.68; V = 3, N = 6, $p = 0.37$).

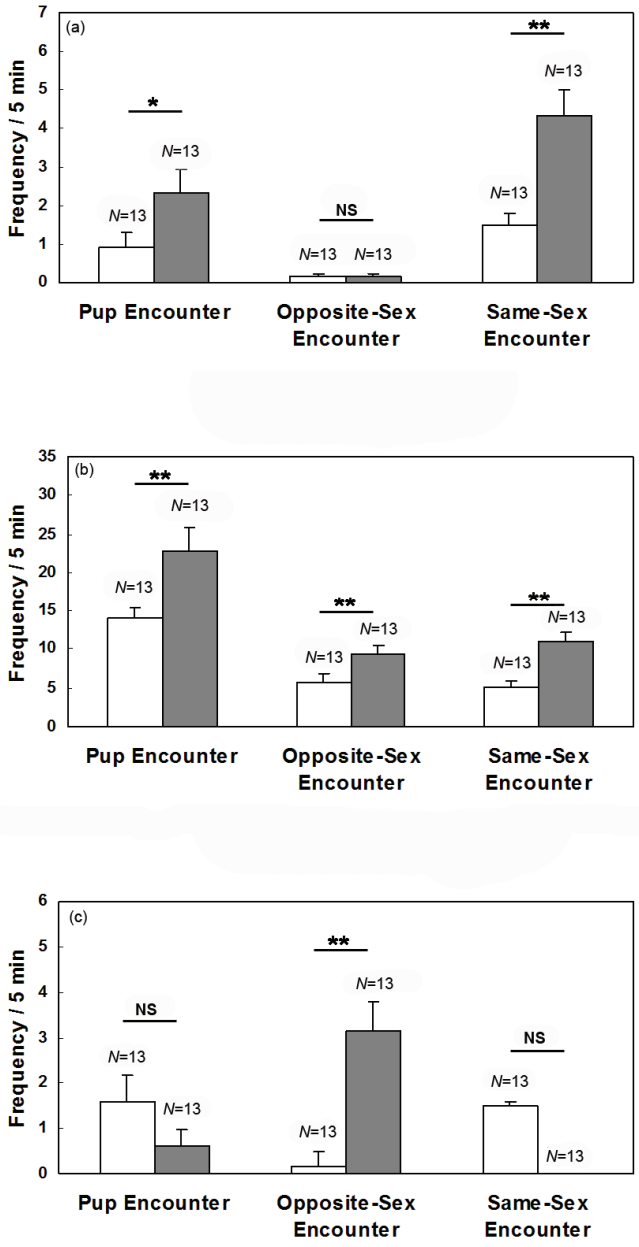

Figure 3.
Behavioural changes in striped mice that became solitary. Striped mice (N = 13) were tested twice, before (in white) and after (in grey) dispersal. Data presented are paired. Mice were presented with pups, same-sex or opposite-sex individuals in a neutral test arena. (a) Aggression, (b) social investigation and (c) amicable behaviours. $**p < 0.01$. Data are presented as mean frequency/5 min ± SE.

(d) Consistency in behavioural traits before and after dispersal

Before and after dispersal, individuals that would later become solitary showed consistency in aggressive behaviour towards pups and same-sex individuals, in social investigation during their encounters with pups, opposite-sex individuals and same-sex individuals and in amicable behaviour towards opposite-sex individuals (Table 1). However, they did not show significant consistency in their aggressiveness towards individuals of the opposite sex or in their amicability towards pups or individuals of the same sex (Table 1).

Before and after dispersal of group members, individuals that remained group-living did not show consistency in any of the behaviours recorded (aggression, social investigation and amicability; Table 1).

Table 1.
Consistency in behavioural traits of group-living and solitary mice before and after dispersal. Consistency in behavioural traits was calculated using Kendall's W coefficient (after Hoset *et al.* 2011). Asterisks denote significant results. P values were adjusted using the Benjamini-Hochberg method.

			N	W	X2	P
Solitary	**Pup Encounter**	*Aggression*	13	0.46	6.0	**0.04***
		Social Investigation	13	0.72	9.3	**0.008***
		Amicable Behaviour	13	0.27	3.57	0.17
	Opposite Sex Encounter	*Aggression*	13	0.00	0.00	0.99
		Social Investigation	13	0.72	9.3	**0.007***
		Amicable Behaviour	13	0.57	7.4	**0.02***
	Same Sex Encounter	*Aggression*	13	0.92	12.0	**0.004***
		Social Investigation	13	1.00	13.0	**0.004***
		Amicable Behaviour	13	0.15	2.0	0.56
Group	**Pup Encounter**	*Aggression*	6	0.50	3.0	0.25
		Social Investigation	6	0.30	1.8	0.37
		Amicable Behaviour	6	0.17	1.0	0.99
	Opposite Sex Encounter	*Aggression*	6	0.17	1.0	0.99
		Social Investigation	6	0.44	2.7	0.22
		Amicable Behaviour	6	0.06	0.3	0.99
	Same Sex Encounter	*Aggression*	6	0.00	0.0	0.99
		Social Investigation	6	0.00	0.0	0.99
		Amicable Behaviour	6	0.33	2.0	0.50

(e) Behavioural syndrome

For mice that were going to become solitary, we found a negative correlation between aggression and amicability towards pups before dispersal took place, with the most

aggressive mice being the least amicable towards pups (Table 2). However, this relationship did not persist after dispersal (Table 2). After dispersal, striped mice never showed amicable behaviours towards same-sex individuals, making calculations of correlation coefficients impossible. We found a positive correlation between social investigation and aggression for same-sex encounters in solitary mice after dispersal (Table 2).

Table 2.
Behavioural syndrome in group-living and solitary mice before and after dispersal. Spearman correlation coefficients between two behavioural traits indicating behavioural syndromes are shown. Asterisks denote significant correlations. NA: all data obtained for amicability towards same-sex individuals were 0; thus it was not possible to calculate a correlation coefficient or a P value for these interactions. P values were adjusted using the Benjamini-Hochberg method.

			Before Dispersal			After Dispersal		
			N	r_s	*P*	*N*	r_s	*P*
Solitary	**Pup Encounter**	*Amicability - Investigation*	16	-0.38	0.38	21	-0.005	0.99
		Aggression - Investigation	16	0.41	0.33	21	-0.089	0.99
		Aggression - Amicability	16	-0.72	0.027	21	-0.26	0.87
	Opposite Sex Encounter	*Amicability - Investigation*	16	0.46	0.25	21	0.3	0.84
		Aggression - Investigation	16	-0.2	0.92	21	0.12	0.99
		Aggression - Amicability	16	-0.49	0.25	21	-0.51	0.13
	Same Sex Encounter	*Amicability - Investigation*	16	-0.23	0.78	21	NA	NA
		Aggression - Investigation	16	0.47	0.25	21	0.69	0.006
		Aggression - Amicability	16	-0.54	0.25	21	NA	NA
Group	**Pup Encounter**	*Amicability - Investigation*	36	0.56	0.003	11	0.78	0.05
		Aggression - Investigation	36	0.13	0.99	11	-0.52	0.49
		Aggression - Amicability	36	-0.17	0.99	11	-0.47	0.54
	Opposite Sex Encounter	*Amicability - Investigation*	36	0.7	0.002	11	0.85	0.02
		Aggression - Investigation	36	0.15	0.99	11	-0.25	0.99
		Aggression - Amicability	36	0.07	0.99	11	-0.27	0.99
	Same Sex Encounter	*Amicability - Investigation*	36	0.35	0.18	11	0.22	0.99
		Aggression - Investigation	36	0.51	0.009	11	0.51	0.49
		Aggression - Amicability	36	-0.06	0.99	11	-0.15	0.99

For mice that would remain group-living, we found a positive correlation between social investigation and amicability for pup encounters and opposite-sex encounters before and after dispersal, suggesting that the most investigative individuals were also the most amicable when they were presented with a pup or an individual of the opposite sex. We also found a positive correlation between social investigation and aggression in group-living mice before dispersal during same-sex encounters.

(f) Factors affecting an individual's behaviour

Aggressive behaviour was significantly influenced by the body mass of the focal mice (heavier individuals were more aggressive; $Z = 4.35$, $p < 0.001$), its sociality (solitary mice were more aggressive than group-living mice; $Z = 3.59$, $p < 0.001$), whether it had dispersed (mice became more aggressive after dispersal; $Z = 2.76$, $p = 0.006$), its age (older mice were more aggressive; $Z = 2.64$, $p = 0.008$) and its reproductive status (sexually mature individuals were more aggressive; $Z = 2.46$, $p = 0.01$). The interactions between dispersal and age ($Z = -2.31$, $p = 0.02$), between dispersal and reproductive status ($Z = -2.19$, $p = 0.03$) and between age and reproductive status ($Z = -2.33$, $p = 0.02$) all positively influenced aggression. Older and sexually mature individuals that became solitary tended to be more aggressive than younger and immature individuals that remained group-living. The sex of the focal mice ($Z = -1.29$, $p = 0.19$) and the stimulus mouse ($Z = 1.27$; $p = 0.20$) did not influence aggression.

Social investigation was significantly influenced by the body mass of the focal mice (heavier individuals were more investigative; $Z = 3.34$, $p = 0.001$), its sociality (solitary individuals were more investigative; $Z = 3.60$, $p < 0.001$) and its sex (males were more investigative than females; $Z = 2.76$, $p = 0.006$). The interactions between body mass and sociality ($Z = -3.74$, $p < 0.001$), between body mass and the stimulus mouse ($Z = -2.98$, $p = 0.003$), between sociality and age ($Z = 2.99$, $p = 0.003$), between dispersal and sex ($Z = -2.64$, $p = 0.008$), between dispersal and the type of stimulus mouse ($Z = -2.71$, $p = 0.007$), between sex and the stimulus mouse ($Z = -2.00$, $p = 0.04$) and between sex and age ($Z = -2.37$, $p = 0.02$) negatively influenced social investigation. Older and heavier females that became solitary were more socially investigative towards pups, whereas older and heavier males that became solitary were more socially investigative towards opposite-sex and same-sex individuals. Dispersal ($Z = -0.68$, $p = 0.49$), stimulus mouse ($Z = -0.92$, $p = 0.36$), age ($Z = -1.82$, $p = 0.07$) and reproductive status ($Z = -0.25$, $p = 0.80$) did not influence social investigation significantly.

Amicability was significantly influenced by sex (males were significantly more amicable than females; $Z = 2.61$, $p = 0.009$), age (younger individuals were more amicable; $Z = -2.04$, $p = 0.04$), whether the focal mice had dispersed (individuals

were more amicable before dispersal; Z = -4.13, $p < 0.001$) and by the type of stimulus mouse presented (focal individuals behaved more amicably according to which mouse was presented to them; in particular they were more sociable to opposite-sex individuals; Z = -3.02, $p = 0.003$). We found significant interactions between sociality and the type of stimulus mouse (Z = -2.54, $p = 0.01$) and between dispersal and the type of stimulus mouse (Z = 2.01, $p = 0.04$). Individuals that became solitary were more amicable towards opposite-sex individuals than individuals that remained group-living. Sociality (Z = 1.95, $p = 0.05$), body mass (Z = 1.16, $p = 0.25$) and reproductive status (Z = -0.43, $p = 0.66$) did not significantly influence amicability.

4. DISCUSSION

Group-living striped mice that dispersed and became solitary changed their behaviour, becoming more aggressive and more investigative. These striped mice already differed in their behaviours from mice that remained group-living before they dispersed, being more aggressive and more investigative. Our study suggests that striped mice are able to adjust their behaviour according to what tactic they follow. This adjustment might occur already before switching tactics or alternatively may result from a predisposition.

Group-living individuals that later became solitary were more aggressive and more investigative than individuals that remained group-living. Previous studies demonstrated that individuals that are more aggressive are more likely to disperse (Myers and Krebs 1971; Kaplan *et al.* 1995; Howell *et al.* 2007). Our results also corroborate the findings of previous studies, which suggested that the tendency to show more exploratory behaviour might develop even before dispersal occurs (Holekamp 1986; Cote *et al.* 2010a; Hoset *et al.* 2011). In group-living species, competition over space and resources is often intense and dominant individuals often reproductively suppress or even evict subordinates (Blumstein and Armitage 1999; Pocock *et al.* 2005; Saltzman *et al.* 2006). In striped mice, there is no indication of eviction events, but there is good indication of reproductive suppression of philopatric males by the male breeder (Schradin *et al.* 2009b) and strong reproductive competition between females (Schradin *et al.* 2010b). In many species dispersal and

onset of solitary-living is a tactic to avoid competition and harassment by dominant group members (Andreassen and Gundersen 2006; Le Galliard 2006; Le Galliard *et al.* 2007). Important differences in dispersal-related behaviours, especially in aggression, already existed in striped mice before dispersal. This was even the case for the comparison between individuals that had experienced the same environment when growing up, that is, individuals that were raised in the same communal litter (mice that later dispersed were more aggressive than their litter siblings that remained in the family group).

Striped mice of both sexes can follow three alternative reproductive tactics: (1) remain as non-breeding philopatric mice within the natal group; (2) disperse and become solitary males or solitary breeding females; or (3) become breeding individuals in a group, which is the natal group in the case of females or a new group in the case of males (Schradin and Pillay 2003; Schradin 2004). Several studies have found an association between exploration and dispersal (Holekamp 1986; Belthoff and Dufty 1998; Dingemanse *et al.* 2003). Accordingly, we found that striped mice became more investigative after they switched from group to solitary-living. It has been suggested that individuals that are more explorative may be able to gather more information from their surroundings (Guillette *et al.* 2009; Rodriguez-Prieto *et al.* 2011). Such information gathering may ultimately allow individuals to assess risks more rapidly (Crusio 2001; Tebbich *et al.* 2009), which can be an advantage when venturing into an unknown environment (Dall *et al.* 2005; Rodriguez-Prieto *et al.* 2011). In all these studies exploration was assessed via open field tests, while we measured social investigation during dyadic encounters. We suggest that an individual that is able to gather social information faster might also be able to react more promptly to competitors or potentially suitable mates that live close to or intrude on to their territory.

Striped mice that became solitary behaved more aggressively to same-sex individuals and pups, but were more amicable to individuals of the opposite sex. Dispersing striped mice are thought to be searching for mating opportunities (Schradin *et al.* 2010a), and thus should be more wary of mice of the same sex, which represent a particular threat as they are reproductive competitors. Hence, males are expected to be more wary of other males as they represent mating competitors, whereas females are expected to be more wary of other females as they compete for access to breeding

territories. Reproductive competition can be high among group-living striped mice, as a single breeding male monopolizes several communally breeding females (Schradin *et al.* 2009c) and suppresses adult male offspring living in the group (Schradin *et al.* 2009c; Schoepf and Schradin 2012). Breeding females show intrasexual aggression and infanticide towards the pups of other females (Schradin *et al.* 2010a). Striped mice of both sexes that become solitary have been shown to be more reproductively successful than group-living philopatric mice (Schoepf and Schradin 2012), success that may stem from their enhanced amicable behaviour towards opposite-sex individuals.

Individuals with particular personality types might find dispersal to be less costly than others and thus may be more successful in settling in a new environment (Clobert *et al.* 2009). Several studies have demonstrated dispersers to differ from non-dispersers in their personality traits; for example, Cote and Clobert (2007) showed that dispersing common lizards, *Lacerta vivipara*, are less sociable than non-dispersing individuals. Duckworth and Badyaev (2007) showed that highly aggressive western bluebirds, *Sialia mexicana*, are more successful at dispersing. Striped mice that became solitary changed their behaviour, but in a consistent manner. In particular, we found that the most aggressive, the most investigative and the least amicable mice were still the most aggressive, the most investigative and the least amicable after they changed their tactic. That dispersing mice differed in behaviour from philopatric mice, and that their behaviour was consistent, implies an important role of personality in the decision to disperse or to remain philopatric. An interesting question would be whether differences in personality traits that influence dispersal probabilities influence fitness. In another publication using data from the same field experiment we demonstrated that striped mice that became solitary were more reproductively successful than striped mice that remained group-living (see Schoepf and Schradin 2012 for more details), indicating that under these environmental conditions differences in personality traits might in fact influence fitness.

In our study we found behavioural syndromes in striped mice that would/did become solitary, syndromes that were not detectable in our small sample of striped mice that remained group-living. A behavioural syndrome consisting of a negative correlation between amicability and aggression was found for the pup encounter test before dispersal, but not after dispersal. A second behavioural syndrome was observed after

dispersal for same-sex individuals and consisted of a positive correlation between aggression and investigation. Dispersing striped mice might be more sexually motivated than striped mice that remained group-living, and sexual motivation might be the proximate cause of dispersal. By dispersing, striped mice are able to escape reproductive suppression and are thus finally able to reproduce (Schoepf and Schradin 2012).

Individuals that live within a family group may be affected both by their parents' and by their siblings' behaviour (Dingemanse *et al.* 2003). Thus, when some group members disperse, this might affect the behaviour of the group members that stay behind. After dispersal of other striped mice, group-living philopatric individuals possibly experienced a less crowded environment and thus had more access to limited resources, such as food, in their territory. However, in our study group-living philopatric striped mice did not change their behaviour significantly after other group members left the group, but a larger sample size would be needed to make a firm conclusion.

Several factors, such as age, weight or reproductive maturity, may affect the behaviour of an individual. For example, several studies on small mammals have found aggressive behaviour to be influenced by sex (Boonstra 1978; Ebensperger 1998; Andreassen and Gundersen 2006). Age has been demonstrated to be an important factor affecting sociability, for example in root voles, *Microtus oeconomus*, which show an increase in asocial behaviour with age (Hoset *et al.* 2011). In our study, we found that striped mice that were heavier, older and had reached sexual maturity were more aggressive. Striped mice switch between tactics depending on their body mass and age: as philopatric mice become older and heavier, they tend to leave the nest and adopt a solitary strategy, with their social status likely to be maintained by aggressive interactions (Schradin and Pillay 2005b; Schradin *et al.* 2009c) as heavier individuals are more likely to win competitive encounters against lighter individuals (Schradin 2004). Reproductive competition has been shown to be the main factor driving striped mice to become solitary with individuals that become solitary being sexually mature more often than individuals that remain philopatric (Schoepf and Schradin 2012).We found solitary heavier individuals to be more socially investigative, and males to be more socially investigative than females, which can be interpreted as their willingness to assess more rapidly whether a strange

individual is a potential competitor or a potential mate, because striped mice males are normally the dispersing sex (Solmsen *et al.* 2011). Philopatric mice choose either to disperse or to remain group-living according to when they are born during the breeding season (Schradin *et al.* 2010a). Individuals that are born early have more chances of finding a suitable area to move into than individuals that are born late as conditions in the field quickly deteriorate as the season progresses. Thus solitary roamers are often also older than males that remain group-living. Sex also had an effect on amicability, with males being less amicable than females and older individuals being less sociable than younger individuals. Dispersal of striped mice typically takes place during the breeding season when food is abundant (Schradin and Pillay 2005a). Males and females might both disperse and become solitary. By the end of the breeding season, roaming males often become group-living by joining a solitary breeding female and her offspring (Schradin *et al.* 2010a). However, in contrast to males, females have never been observed joining other groups of females. Striped mice were more sociable towards opposite-sex individuals than towards pups or same-sex individuals. Competition for mating partners and space is expected to be stronger between individuals of the same sex (Le Galliard 2006), and striped mice of both sexes compete fiercely with other individuals of the same sex (Schradin 2004), and are expected to be less tolerant and thus less sociable towards individuals of the same sex than they are towards individuals of the opposite sex that might always represent a potential mate instead.

Few other studies have examined the potential link between specific behaviours, such as aggression, social investigation and amicable behaviour, and their repercussion on the social tactic of an individual. Our results indicate that solitary striped mice differ in behavioural traits from group-living striped mice, and these behavioural differences are already present before the solitary tactic is adopted. Behavioural traits such as exploration, aggression and amicability may influence the chances of individuals succeeding in a new environment and they may ultimately determine its reproductive success. It would be interesting to study whether closely related species that differ in sociality (solitary versus group-living) differ in the same personality traits as do solitary and group-living striped mice. The decision to disperse and become solitary seemed to be driven by increased aggressive behaviour towards same-sex individuals and increased amicable behaviours towards opposite-sex individuals, both being

indicators of sexual motivation. Our study provides evidence not only that individuals that disperse and become solitary differ behaviourally from their group-living counterparts, but also that these differences are already present even before the dispersal event.

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CHAPTER 3

Endocrinology of sociality: comparisons between sociable and solitary individuals within the same population of African striped mice

Hormones and Behavior

In press

Endocrinology of sociality: comparisons between sociable and solitary individuals within the same population of African striped mice

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Abstract

The social organization of species ranges from solitary-living to complex social groups. While the evolutionary reasons of group-living are well studied, the physiological mechanisms underlying alternative social systems are poorly understood. By studying group-living and solitary individuals of the same species, we can determine hormonal correlates of sociality without the problem of confounding phylogenetic factors. The African striped mouse (*Rhabdomys pumilio*) is a socially flexible species, which can be solitary or alternatively form complex family groups, depending on population density and the extent of reproductive competition. We predicted group-living striped mice to show signs of reproductive suppression and social stress, resulting in higher corticosterone but lower testosterone levels when compared to solitary-living individuals. To determine whether differences in social organization correlated with hormonal differences, we collected blood samples from free-living striped mice during four breeding seasons when we experimentally induced solitary-living in philopatric individuals by locally reducing population density. Striped mice that were group-living did not change their corticosterone or testosterone levels during the study, indicating that there was no temporal effect during the breeding season. Striped mice of both sexes had significantly lower corticosterone levels after switching from group- to solitary-living. Solitary males – but not solitary females –had higher testosterone levels than group-living conspecifics. Our results suggest that group-living results in physiological stress and can induce reproductive suppression, at least in philopatric males. The switch to solitary-living may thus be a tactic to avoid reproductive competition within groups,

and is associated with decreased stress hormone levels and onset of independent reproduction.

Key-words: aggression; dispersal; social flexibility; philopatry; communal breeding; cooperative breeding; alternative reproductive tactics; helper.

1. INTRODUCTION

Animals show a variety of different social organizations, ranging from species that live solitarily to species that form complex social groups (Wilson 2000). Solitary and group-living species display distinct mating systems, which are believed to arise as a consequence of differences in individuals' social interactions with their conspecifics (Blumstein *et al.* 2010). The ecological and evolutionary reasons that cause individuals to form and maintain social groups have been extensively studied (Koenig *et al.* 1992; Emlen 1995; Cahan *et al.* 2002), while the reasons of solitary-living have received less attention (Schradin *et al.* 2012b). More recently, it has been shown that relaxed ecological constraints (low population density) and high reproductive competition within groups favour solitary-living (Schradin *et al.* 2010; Schoepf and Schradin 2012a), supporting previous findings (Koenig *et al.* 1992) and theory (Emlen 1995). In comparison, the underlying physiological mechanisms that lead to different forms of social systems are still poorly understood.

Many studies of the proximate mechanisms of sociality have focused on the neuro-endocrine system (Pfaff 2005; Schoech *et al.* 2004). Hormone levels can change in a relative short period (Wynne-Edwards and Reburn 2000) and, by acting directly in the brain and on the peripheral organs, play a prominent role in affecting an individual's behaviour (Buntin 1996). Glucocorticoids (e.g. corticosterone) are important modulators of stress responses as they allow individuals to react to energetically demanding situations, such as those encountered during social interactions, dispersal and when exploring novel environments (Belthoff and Dufty 1998; Creel 2001; Young and Monfort 2009). Androgens (e.g. testosterone) are strong modulators of reproduction, dominance and aggression (Moore *et al.* 1998; Evans *et al.* 2000). Most of the endocrinological research on sociality has thus far focused on comparing dominants and subordinates within the same group (Poiani and Fletcher 1994; Carlson *et al.* 2004; Malueg *et al.* 2009) or on the role of hormones in group stability (Sapolsky 1992) and intraspecific encounters (Marler *et al.* 1995). What is so far mainly missing are comparisons between solitary and group-living individuals. Solitary and group-living species are expected to differ in the way they react to environmental limitations, yet comparisons of physiological mechanisms of solitary and group-living species are very rare and difficult to interpret because of confounding phylogenetic effects (Beery *et al.* 2008). Studies on endocrine factors of

dispersal (Nunes *et al.* 1999) are problematic as in most social species individuals are solitary only during the dispersal phase and do not follow a permanent solitary tactic. These problems could be avoided by studying the physiological profiles of socially flexible species.

In socially flexible species, both group-living and solitary individuals occur in the same population, and even the entire social organization of a population can switch from group- to solitary-living as a response to environmental changes (Schradin *et al.* 2012b). Social flexibility has been observed in several species of insects, birds and mammals where both males and females are able to change their social and reproductive tactics in response to changing environmental conditions (Schradin *et al.* 2012b). Studies of species with alternative reproductive tactics indicate that individuals following different tactics differ in their steroid hormone levels (Oliveira *et al.* 2008). Males following a dominant bourgeois tactic also often have the highest androgen levels (Rose *et al.* 1971; Bartsch *et al.* 1992; Gould 2005), whereas glucocorticoid patterns are not as clear because subordinate individuals of some species show high glucocorticoid levels (Creel 2005), whereas in other species, individuals following a dominant tactic have the highest glucocorticoid levels (Creel 2001). Nonetheless, individuals following alternative reproductive tactics differ in their hormone profile, and we can thus expect hormonal differences also between group-living and solitary individuals of the same species.

The African striped mouse (*Rhabdomys pumilio*) is a highly socially flexible species, and thus makes for an ideal model to study whether individuals that are solitary differ in their hormone profile from individuals that are group-living. When population density is high, striped mice live in extended family groups, consisting of a breeding male, two to four communally breeding females and their adult philopatric offspring of both sexes (Schradin and Pillay 2004). Individuals of both sexes can become solitary if population density becomes low during the breeding season (Schradin *et al.* 2010b; Schoepf and Schradin 2012a). Striped mice of both sexes are thus able to follow one of three alternative reproductive tactics: (i) remain as non-breeding philopatrics in their natal nest; (ii) become dominant group-living breeders; or (iii) disperse and become solitary-living breeding females or solitary roaming males (Schradin and Pillay 2003; Schradin 2004). Corticosterone levels of non-breeding philopatric striped mice are seven times higher than those of breeding males during

the breeding season, but these levels drop in the non-breeding season (Schradin 2008), or when males are removed from the family in captivity, indicating that philopatric males are reproductively suppressed (Schradin *et al.* 2009b; Schradin *et al.* 2012b). Intra-group competition over limited resources, such as food, can be high in group-living species (Danchin *et al.* 2008) and may cause additional physiological stress, which might be reduced when group size declines. Dispersal of siblings causes a decline of group size and might influence the hormone profile of those individuals remaining within the group. We predicted: a) group-living striped mice of both sexes that would later become solitary to have higher corticosterone levels than their siblings which would remain group-living (i.e. high corticosterone levels could trigger dispersal), b) corticosterone levels to decrease once individuals have dispersed and have become solitary; and c) group-living individuals to show lower corticosterone levels after group size declined due to the dispersal of other group members.

Testosterone levels of male philopatrics are lower than those of roaming and breeding males (Schradin *et al.* 2009a), and testosterone levels of all male and female striped mice decrease from the breeding to the non-breeding season (Schradin 2008). Testosterone promotes sexual motivation and suppresses parental care in males (Wingfield *et al.* 1990; Ketterson and Nolan 1999; Wingfield *et al.* 2001). Philopatric striped mice act as helpers at the nest and show high degrees of alloparental care, whereas solitary-living roaming males do not participate in parental care (Schradin *et al.* 2009a). Testosterone has been associated with aggression in males (Wingfield *et al.* 1990) and in many vertebrate species females can be as aggressive as males (Hau 2007), including striped mice, in which individuals of both sexes are more aggressive when they become solitary than when they are group-living (Schoepf and Schradin 2012b). In addition, testosterone is anxyolytic in laboratory mice (Aikey *et al.* 2002) and might promote risk-taking in roaming male striped mice (Schradin *et al.* 2009b). Female striped mice can either breed communally or solitarily, with solitary-breeding likely to be the riskier tactic, since solitary breeders must find and defend a territory alone. Thus, testosterone in females might play a similar role as in males in promoting risk-taking behaviours. We predicted: a) testosterone levels of solitary individuals of both sexes to be higher than of group-living individuals; and b) testosterone levels of males and females that would later disperse to be higher than those of individuals that would remain group-living, indicating their readiness to seek independent breeding.

2. MATERIAL AND METHODS

(a) Study period and field techniques

Data were collected during the breeding season (August to November) of 2007-2010 on a field site located on the farm Klein Goegap (29°42.30'S - 18°02.95'E) near the town of Springbok in South Africa. Striped mice social tactics (solitary or group-living) were determined using a combination of trapping, radio-tracking and behavioural observations (Schradin *et al.* 2010b; Schoepf and Schradin 2012a). Striped mice were trapped at their nest, sexed, weighed and marked permanently with ear-tags (National Band and Tag Co., Newport, KY, U.S.A.) and temporarily with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa) for individual recognition during behavioural observations. All adult breeders and up to four philopatrics (two females and two males) of each group were fitted with radio-collars (Holohil, Carp, Ontario, Canada; 1.2-4.5g). Striped mice were radio-tracked during the day to determine home ranges and at night to determine composition of sleeping groups, following the methods previously established by Schradin and Pillay (2005). Striped mice that spent more than 75% of the nights with other individuals were regarded as group-living whereas those that slept alone for >75% of the nights were regarded as solitary-living; no intermediate values occurred. All mice sampled were part of a field manipulation experiment in which we tested the role of population density on sociality by removing several groups from the field site (Schoepf and Schradin 2012a). Removal of groups was carried out in the beginning of each breeding season in the years 2007 to 2010. Altogether, 52 mice from 12 groups were removed from a 30 hectares area (for more details see Schoepf and Schradin 2012a). Blood samples were obtained only from individuals belonging to groups that were not removed.

(b) Collection and analysis of blood samples

Striped mice were captured directly at their nests in the early morning (between 06:15 and 8:30 depending on sunrise) within 30min after they emerged. Mice were anaesthetized with diethyl ether and blood samples were collected from a sublingual vein (Heimann *et al.* 2009). All samples were obtained within three minutes after a mouse had entered the traps to avoid a stress response (Schradin 2008). Samples were

transported to the research station, where they were left to clot at room temperature (for up to 1.5h from the time the sample was taken; ambient temperature was mainly below 20 ºC during the breeding season). Samples were centrifuged for 10 minutes and the obtained serum (extracted in different aliquots: 20 µl for corticosterone and 60 µl for testosterone) was stored at -20 ºC. All samples were analyzed at the University of Zurich, using enzyme immuno-assays. Corticosterone and testosterone levels were measured with commercial kits from IBL Hamburg, following procedures previously validated for striped mice (Schradin 2008). Coefficients for intra-assay variation were 7.8% for testosterone and 11.1% for corticosterone. Coefficient for inter-assay variation was 10.2% for testosterone and 10.9% for corticosterone. 30 samples from group-living mice and 30 samples from solitary mice were analyzed for corticosterone, and 27 samples from group-living individuals and 31 samples from solitary individuals were analyzed for testosterone (Table 1).

			Before	After
Corticosterone	**Philopatric**	*Male*	6	7
		Female	12	5
	Solitary	*Male*	5 (2)	11 (2)
		Female	5 (4)	9 (4)
Testosterone	**Philopatric**	*Male*	4	10
		Female	8	5
	Solitary	*Male*	5 (2)	12 (2)
		Female	5 (3)	9 (3)

Table 1.
Total number of males and females sampled for corticosterone and testosterone throughout the study. "Philopatric" indicate individuals that remained permanently group-living and "Solitary" individuals that were originally group-living, but later became solitary. Numbers in parenthesis indicate individuals that were sampled twice.

Blood samples were obtained an average of 8.55 ± 5.25 days before individuals switched from group-living to solitary and an average of 9.78 ± 5.77 days after individuals had become solitary. Six individuals (four females and two males) were re-sampled after switching from group-living to solitary. We waited 16.00 ± 3.94 days before taking blood from the same individual. All individuals used in the study were initially philopatrics, born from the first litter of the breeding season and, thus, of

similar age and body mass when sampled. The study obtained ethical clearance from the University of the Witwatersrand (AESC: 2007/38/04).

Figure 1.
Collection of blood samples from striped mice was obtained directly in the field as individuals emerged from their nests to minimize handling time.

(c) Data analysis

Data analysis was performed using the statistical software R (version 2.11.0 R Development Core Team 2006). Data were tested for normality using the Shapiro-Wilk Normality Test and are presented as mean ± standard deviation. Exact p-value calculations were performed on all tests. We used generalized linear models (GLM) to compare: 1. group-living mice that remained so, with mice that would become solitary-living, before the latter dispersed; and 2. mice that remained group-living and mice that became solitary after dispersal of the latter. The first GLM was used to test whether striped mice that would later become solitary already differed hormonally from striped mice that remained group-living before dispersal. The second GLM tested whether group- and solitary-living individuals differed in hormone levels after dispersal. Each GLM had one of the hormones (corticosterone or testosterone) as the response variable; while sex and social category (group-living or solitary) were the fixed factors. We used linear mixed effect models (LMM) to compare: (i) striped mice that became solitary-living, before and after dispersal; and (ii) striped mice that remained group-living, before and after the dispersal of some of their group members. The first LMM was used to test whether striped mice change their hormone levels when they change social tactic. The second LMM was used to test whether hormone

levels of group-living individuals might change following the departure of some of their group members even though their social tactic did not change. Each LMM had one of the two hormones as the response variable, sex and social category as the fixed factors and individual ID as a random factor to account for pseudo-replication. We selected the best model by a stepwise backward procedure (following Crawley 2007). Hormone levels were square-rooted or log-transformed prior to analyses owing to their skewed distribution. We used LMMs and GLMs to compare hormone levels between subjects and paired t-tests to compare hormone levels within the same individuals before and after they became solitary.

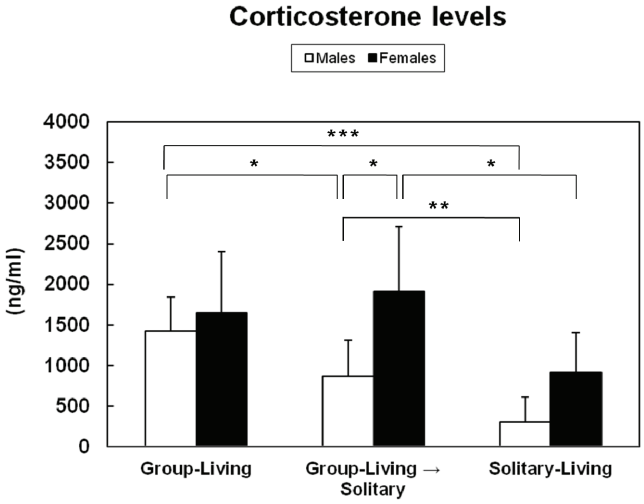
3. RESULTS

(a) Differences in hormone levels between permanently group-living striped mice and group-living striped mice that later became solitary-living

Group-living striped mice males that would later become solitary displayed a trend towards having lower corticosterone levels than males that would remain group-living (GLM: $F_{1, 9} = 4.6$, $p = 0.06$; Fig. 1a). Group-living striped mice females that would later become solitary did not differ in their corticosterone levels from females that remained group-living (GLM: $F_{1, 16} = 0.48$, $p = 0.50$; Fig. 1a). Dispersing males' corticosterone levels were significantly lower than those of dispersing females (GLM: $F_{1, 9} = 5.50$, $p = 0.04$; Fig. 1a), whereas corticosterone levels of striped mice males and females that remained group-living did not differ (GLM: $F_{1, 16} = 0.43$, $p = 0.52$; Fig. 1a).

Group-living striped mice males that would later become solitary did not differ in their testosterone levels from males that would remain group-living (GLM: $F_{1, 7} = 0.33$, $p = 0.58$; Fig. 1b); and group-living striped mice females that would later become solitary did not differ in their testosterone levels from females that would remain group-living (GLM: $F_{1, 11} = 2.43$, $p = 0.15$; Fig. 1b). Whereas dispersing males' testosterone levels did not differ significantly from those of dispersing females (GLM: $F_{1, 8} = 0.13$, $p = 0.72$; Fig. 1b), non-dispersing males had higher testosterone levels than non-dispersing females (GLM: $F_{1, 10} = 9.62$, $p = 0.01$; Fig. 1b).

a)



b)

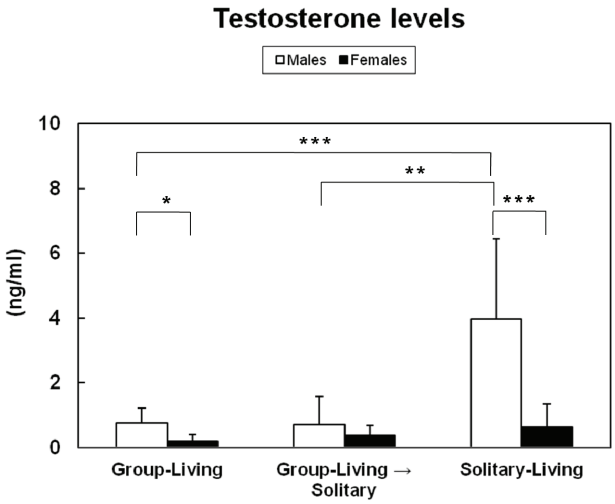


Figure 1.
Comparison of hormone levels between permanently group-living mice (labelled as 'Group-living'), group-living mice that later became solitary (labelled as 'Group-living → Solitary'), and, solitary-living mice (labelled as 'Solitary'). a) Corticosterone and b) Testosterone. p* < 0.05; p** < 0.01; p*** < 0.001.

(b) Comparison of hormone levels between solitary individuals before and after they became solitary

We compared hormone levels of mice that were group-living at the start of the experiment but later became solitary (middle bars of Fig. 1) with hormone levels of solitary mice at the end of the experiment (right bars in Fig. 1). Striped mice that were group-living at the start of the experiment but later became solitary had significantly

higher corticosterone levels than solitary-living striped mice (at the start of the experiment: 1437.85 ± 832.44 *vs.* at the end of the experiment: 575.62 ± 497.13; LMM: $F_{1, 5} = 16.73$, $p = 0.009$). Specifically, males that were group-living at the start of the experiment, but would later become solitary, had significantly higher corticosterone levels than solitary-living males (GLM: $F_{1, 14} = 7.04$, $p = 0.02$; Fig. 1a); and females that were group-living at the start of the experiment, but would later become solitary, had significantly higher corticosterone levels than solitary-living females (LMM: $F_{1, 3} = 11.64$, $p = 0.04$; Fig. 1a). Corticosterone levels of males were significantly lower than females both at the start (GLM: $F_{1, 9} = 5.50$, $p = 0.04$; Fig. 1a) and at the end of the experiment (GLM: $F_{1, 18} = 10.30$, $p = 0.005$; Fig. 1a).

Male striped mice that were group-living at the start of the experiment but later became solitary had significantly lower testosterone levels than solitary-living males (GLM: $F_{1, 14} = 13.16$, $p = 0.003$; Fig. 1b). Testosterone levels of females that were group-living at the start of the experiment but later became solitary remained similar to those of solitary-living females (LMM: $F_{1, 3} = 1.15$, $p = 0.30$; Fig.1b). While testosterone levels of males that would become solitary did not differ from females that would become solitary at the start of the experiment (GLM: $F_{1, 8} = 0.13$, $p = 0.72$; Fig. 1b), solitary-living males had significantly higher testosterone levels than solitary-living females (GLM: $F_{1, 18} = 32.65$, $p < 0.0001$; Fig. 1b).

In addition, we compared changes in hormone levels for six individuals (four females and two males for corticosterone and three females and two males for testosterone) for which we had samples when they were still in the group and after they had become solitary (paired data). Striped mice that dispersed and adopted a solitary life significantly decreased their corticosterone levels (before: 1427.59 ± 1020.01 *vs.* after: 664.74 ± 681.68; t = 2.28, df = 5, $p = 0.04$). Testosterone levels increased considerably in both males (male 1 increased from 0.33ng/ml to 5.55 ng/ml and male 2 increased from 0.80 ng/ml to 1.06 ng/ml), and in three out of four females (from 0.37 ± 0.41 to 1.03 ± 1.17).

(c) Hormonal adjustment in group-living individuals following dispersal of group members

Corticosterone levels of both group-living striped mice males and females remained similar after the departure of some of their group members (males before: 1426.00 ± 420.28 *vs.* after: 1382.29 ± 622.40; GLM: $F_{1, 11} = 0.02$, $p = 0.89$; females before: 1645.67 ± 756.25 *vs.* after: 1504.82 ± 780.39; LMM: $F_{1, 3} = 0.11$, $p = 0.79$).

Testosterone levels of group-living females showed a trend towards increasing following the departure of some of their group-members (before: 0.19 ± 0.20 *vs.* after: 0.60 ± 0.52; GLM: $F_{1, 11} = 4.30$, $p = 0.06$), while testosterone levels of group-living males remained similar even after the departure of some of their group members (before: 0.77 ± 0.45 *vs.* after: 0.54 ± 0.48; GLM: $F_{1, 12} = 1.03$, $p = 0.33$).

(d) Differences in hormone levels between individuals that remained group-living and individuals that became solitary after dispersal of the latter

Solitary striped mice males had significantly lower corticosterone levels than their conspecifics that remained group-living (solitary: 301.12 ± 304.22 *vs.* group-living: 1382.29 ± 622.40; GLM: $F_{1, 16} = 26.72$, $p < 0.0001$) and significantly higher testosterone levels (solitary: 3.85 ± 2.39 *vs.* group-living: 0.54 ± 0.48; GLM: $F_{1, 20} = 41.71$, $p < 0.0001$). Solitary females did not differ in their corticosterone (solitary: 911.11 ± 490.96 *vs.* group-living: 1504.82 ± 780.39; GLM: $F_{1, 12} = 2.88$, $p = 0.11$) and in their testosterone levels from females that remained group-living (solitary: 0.63 ± 0.71 *vs.* group-living: 0.60 ± 0.52; GLM: $F_{1, 12} = 0.02$, $p = 0.88$).

4. DISCUSSION

Striped mice that became solitary had significantly lower corticosterone levels than individuals that remained group-living, suggesting that adopting a solitary tactic can be a way to avoid social stress arising from group-living. Males that left their natal group to become solitary increased their testosterone levels but not males that remained group-living. Females that became solitary decreased their corticosterone levels significantly, but did not increase in their testosterone levels. In a previous

study, we demonstrated that males that dispersed were scrotal while males that remained philopatric in their natal group were unscrotal; and that 75% of females that dispersed, but only 13% of females that remained philopatric were breeding (Schoepf and Schradin 2012a). Our results show that group-living males and females differ considerably in their hormone profiles from solitary-living males and females and indicate that hormone levels change when striped mice switch from group- to solitary-living.

Glucocorticoids affect reproductive behaviour by regulating the availability of energy by influencing glucogenesis, fat and protein metabolism (Romero 2002; Reeder and Kramer 2005). In some group-living birds and mammals, dominant individuals have higher glucocorticoid levels than subordinates, while in other species dominants have lower levels. This difference might depend on whether it is more stressful to occupy a dominant or a subordinate rank (Creel 2001). One suggestion is that dominant individuals suppress the reproduction of subordinates by inducing chronic stress, resulting in sustained high levels of glucocorticoids in subordinates (Abbott *et al.* 2003; Reyer *et al.* 1986). Our results taken together with results from previous studies (Schradin 2008; Schradin and Yuen 2011; Schradin *et al.* 2009b; Schradin *et al.* 20012b; Schradin *et al.* 2012c) indicate that this is the case in philopatric male striped mice. Chronically increased glucocorticoid levels indicate allostatic load, i.e. physiological costs due to an over activation of the neuroendocrine stress response (McEwen and Wingfield 2003). As a consequence, philopatric males should leave their natal group when costs of dispersing to become solitary are lower than costs of remaining philopatric. By reducing population density we experimentally offered such option. In our study, corticosterone levels of solitary males only showed a trend towards decreasing before these individuals changed from group-living to solitary. While corticosterone levels of males became significantly lower after individuals switched from a social to a solitary tactic. The difference in corticosterone levels between individuals that switched from group- to solitary-living was much more marked than the difference between individuals that were initially group-living but later became solitary and individuals that remained group-living. Additionally, males that switched tactic were already sexually mature before dispersal (Schoepf and Schradin, 2012a), which is in agreement with the observation that high testosterone

levels are not compatible with high corticosterone levels in this species (Raynaud *et al.* 2012).

After becoming solitary, females retained significantly higher corticosterone levels than males, indicating important physiological differences between the sexes. In mammals, breeding females need high glucocorticoid levels to deal with the energetic demands of lactation and pregnancy (Reeder and Kramer 2005), and in striped mouse breeding females have high corticosterone levels (Schradin 2008). Nevertheless, also in female striped mice high corticosterone levels could be an indicator of stress, including social stress and our present study found that females that switched from group- to solitary-living decreased their corticosterone levels. Most importantly and, in contrast with philopatric males, philopatric females can breed in their natal group when population density is low (Schradin *et al.* 2010). In an accompanying study we showed that females that 75% of females that became solitary reproduced, but only 13% of females that remained group-living bred (Schoepf and Schradin 2012a,b). Thus, increased corticosterone levels due to social stress could be one explanation why young philopatric females often do not breed, but this needs further investigation, particularly as our results showed that females that remained philopatric did not differ in their corticosterone levels from females that became solitary. The situation in females seems to be thus more complex than in males and further studies are needed to elucidate it.

Dispersal of individuals from a group might affect others that remain in the group. Dispersal of siblings has been shown to reduce competition over food and to increase body condition in screech-owls (*Otus asio* and *Otus kennicottii*; Belthoff and Dufty 1998). In our study, dispersal of group-members did not cause changes in corticosterone levels in the individuals that remained group-living, suggesting that a decrease in group size did not decrease stress levels, supporting the idea that remaining as a non-breeding helper within the group is stressful.

Group-living striped mice that later became solitary did not differ in their testosterone levels from striped mice that would remain group-living. Testosterone levels of philopatric males also remained similar before and after departure of some of their group-members, suggesting that reproductive suppression by their father rather than other factors, such as population density, is the cause of their retained low

testosterone levels. Testosterone levels of solitary males, however, significantly increased. Similarly, previous research has shown that philopatric male striped mice that become solitary roaming males increase their testosterone levels and decrease their corticosterone levels (Schradin and Yuen 2011). In males, testosterone has several functions, which among others include the regulation of aggression, sexual behaviour and dispersal (Ketterson and Nolan 1999; Wingfield *et al*. 2001; Nelson 2005). Testosterone levels of solitary males in our study were comparable to testosterone levels measured in solitary males following a roaming tactic (Schradin *et al.* 2009a). Philopatric males normally have smaller testes and lower sperm counts (Schradin *et al.* 2009b), as well as lower testosterone and higher corticosterone levels than roaming males (Schradin *et al.* 2009a). Striped mice dispersed to seek independent breeding opportunities as soon as free territories were made experimentally available (Schoepf and Schradin 2012a). While most philopatric males are sexually suppressed, males that dispersed were already sexually mature (i.e. scrotal) at the time of dispersal (Schoepf and Schradin 2012a). Thus, physiological changes might have been initiated already shortly before dispersal. However, our current study demonstrates that these physiological changes did not occur before we manipulated the environment and made territories available. Thus, it is likely that an increase of testosterone levels shortly before dispersal might trigger the switch from group- to solitary-living.

Testosterone levels of females were very similar to testosterone levels of philopatric males, independently of their dispersal status, and comparable to those shown in a previous study (Schradin 2008). In contrast to males, female testosterone levels did not increase significantly after dispersal and stayed in a low but measurable range. One of the many functions of testosterone is to promote sexual motivation in males (Ketterson and Nolan 1999; Wingfield *et al.* 1990), while its functions in female vertebrates are poorly understood. Testosterone in female mammals may also, as it is in male, be associated with dispersal (Holekamp *et al.* 1984; Nunes *et al.* 1999), and there are increasing evidence, at least in some species, that in the absence of reproductive suppression testosterone levels can become higher even in females (Lutermann *et al. in press*). In our study, females that dispersed and became solitary had nearly double as high testosterone levels as philopatric females, but this difference was not significant and overall testosterone levels of solitary females were

low. The lower testosterone levels in females as compared to males might indicate that in female striped mice testosterone is not as important in reproduction as it is for males. Like in males, females that became solitary started breeding, while most females that remained philopatric did not (Schoepf and Schradin 2012a), providing evidence that other hormones rather than testosterone might play an important role in dispersal (perhaps progesterone or oestrogen, which were not studied here, due to the small amounts of serum available). Interestingly, females' testosterone levels increased following the departure of some of their group-members, but did not become higher than those of females that became solitary-living, and, at the moment, it is not clear whether the significant increase we observed has any biological significance, especially as testosterone levels were still relatively low.

Our results revealed important insights into the physiological mechanisms underlying the differences between group-living and solitary individuals. Dispersing males had lower corticosterone levels than philopatric males. As breeding males need low corticosterone levels to allow for high testosterone levels necessary for spermatogenesis (Raynaud *et al.* 2012), this might indicate that these males were already physiologically primed to disperse and start independent breeding. Corticosterone levels were much lower in solitary striped mice of both sexes. High corticosterone levels indicate high physiological and metabolic costs for group-living individuals. Solitary males had significantly higher testosterone levels than group-living males, suggesting that they were no longer reproductively suppressed. Ours is one of very few studies comparing hormone levels between alternative social and reproductive tactics in both sexes. Taken together with previously published results (see Schoepf and Schradin 2012a, b) our findings indicate a link between environmental change, behavioural adaptation and underlining physiological mechanisms, which result in significant fitness consequences.

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CHAPTER 4

Experimental manipulation of the number of neighbours and the availability of food resources affects home range size of female African striped mice (*Rhabdomys pumilio*)

To be submitted

Experimental manipulation of the number of neighbours and the availability of food resources affects home range size of female African striped mice (*Rhabdomys pumilio*)

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To be submitted

Summary

1. An individual's home range determines its access to resources, significantly influencing its survival, reproduction and ultimately its fitness.

2. Several correlative studies have shown that a variety of factors influence home range sizes Resource availability and population density have been considered to be among the most important determinants of animal space use patterns.

3. While there has been a profusion of observational and a few experimental studies investigating the influence of food availability or population density on home range sizes, none so far has experimentally tested the two factors together in a single study.

4. Many studies have shown home range sizes to be negatively correlated with both resource availability and population density, but as these two factors normally correlate positively with each other, it has been so far difficult to differentiate the effect of one from the other. To determine the extent of these two factors on home range patterns, it is thus important to design experiments in such a way where one factor can be varied while the other is held constant.

5. Using two separate field manipulation experiments, we tested whether resource availability and population density affect home range sizes and home range overlap of female striped mice (*Rhabdomys pumilio*).

6. In a first experiment, we manipulated resource availability by providing supplemental food for a short period of eight weeks to 23 females belonging to 15 different groups. To avoid immigration into the study area and thus control for population density we provided food to neighbouring groups as well. While population density did not increase, female home range sizes decreased by approximately 25%.

7. In a second experiment, we manipulated population density by removing groups of mice. Experimental decrease of population density caused an increase of female home range sizes by approximately 40% within seven weeks, a period short enough to control for a change in food availability.

8. In contrast with previous studies, female striped mice did not shift their home range but mostly used the same area throughout the study underlining the importance of site fidelity and territoriality in this species.

9. The degree of home range overlap between female striped mice was not influenced by neither food presentation or by reduction of population. However, female home range sizes were negatively affected by the number of female neighbours, indicating that females try to minimize direct competition with same-sex neighbours even when enlarging their home range.

10. Following removal of neighbours, home range sizes of females associated with a breeding male significantly increased, while the overlap with neighbouring males, particularly with solitary roamers, decreased indicating that individuals of the opposite-sex might be more important in affecting space use patterns of females than previously thought.

11. This is the first comprehensive field manipulation study of a single species that has been able to extrapolate the actual effects that an increase in food availability and a decrease in population density have on home range sizes and space use patterns by singling out one factor while controlling for the other one.

Key-words: home range, food manipulation, population density, resource availability, spatial use.

1. INTRODUCTION

A home range is the area inhabited by and individual over a given time that contains the necessary resources, such as feeding sites and nesting areas, which ensure its survival and reproduction (Burt 1943), significantly influencing its fitness (Bowler and Benton 2009). Variation in home range sizes can be high, even within the same population (Schradin *et al.* 2010c). Crucially, home ranges do not need to be exclusive and therefore home ranges of several individuals can overlap. Several factors may be responsible for variation in home range characteristics between individuals. For example, sex, age, body mass, cover availability and seasonal climatic conditions can affect intraspecific variation in home range sizes and overlap with other individuals (Ostfeld 1990; Mikesic and Drickamer 1992; Tufto *et al.* 1996; Priotto *et al.* 2002; Hayes *et al.* 2007; Hoset *et al.* 2008; Schradin *et al.* 2010c). Ultimately, however, the fitness of an individual is limited by the availability of resources within its territory and by the number of conspecifics it needs to compete against to secure access to said resources (Lopez-Sepulcre and Kokko 2005; Schradin *et al.* 2010c).

Several studies have shown that home range size is negatively correlated with food availability probably because when food is more abundant, an individual needs less space to acquire sufficient energy to survive and reproduce (Travis and Slobodchikoff 1993; Tufto *et al.* 1996; Saïd *et al.* 2005). This idea has been supported by a few experimental studies, where food availability was manipulated. For example, food provisioning caused a reduction of home range sizes in grey-sided voles (*Clethrionomys rufocanus*; Ims 1987) and in arctic ground squirrels (*Spermophilus parryii*; Hubbs and Boonstra 1998), but had no effect in degus (*Octodon degus*; Hayes *at al.* 2007). Artificially provisioned food has also been shown to cause an increase in home range overlap in California voles (*Microtus californicus*; Ostfield 1986) and grey-sided voles (Ims 1987). Food availability is thus an important factor affecting home range parameters; consequently animals may try and occupy home ranges that are larger than their needs.

A large home range that includes a great amount of resources may lead to higher fitness, and as a result an individual should aim to secure as many resources for itself and its offspring as possible (Stamps 1994; Adams 2001; Lopez-Sepulcre and Kokko

2005). However, an area that includes a large number of resources may attract potential competitors. Numerous correlative (Ostfeld *et al.* 1985; Erlinge *et al.* 1990; Agrell 1995) and experimental studies (Lovallo and Anderson 1995; Koskela *et al.* 1999; Baker *et al.* 2000) have shown that home range sizes decrease when population density increases (but see Ostfeld 1986; Mares and Lacher 1987; Sera and Gaines 1994 for some noticeable exceptions). Thus, the provisioning of additional food in experimental studies may attract a greater number of immigrants within the area leading to enhanced competition because of increased population density (Taitt and Krebs 1981; Hews 1993; Perrin and Johnson 1999). In studies where population density was controlled, a change in food availability was either negatively correlated (Mares *et al.* 1982) or not correlated (Vlasman and Fryxell, 2002) with home range size.

An increase in population density is also often associated with an increase in home range overlap between individuals (Ostfeld *et al.* 1985; Ims 1987). Sharing parts of the home range with other individuals implies sharing food resources and, thus, individuals that do so are expected to require a larger home range to meet the necessary energy requirements (Buskirk 2004). This in turn can further increase competition with neighbouring individuals. When neighbours were removed or had disappeared, the remaining individuals enlarged their home ranges (Boutin and Schweiger 1988; Lovallo and Anderson 1995; Baker *et al.* 2000). This indicates that social interactions with neighbouring individuals prior to removal could have constrained remaining individuals in their space use patterns (Jetz *et al.* 2004). Population density is therefore an important determinant of the frequency and intensity of intraspecific aggression, which tends to increase as food becomes scarcer (Stamps and Buechner 1985; Eberhard and Ewald 1994; Luna and Baird 2004). Understanding the effects that the availability of resources and the presence of competitors bear on animal space use is then critical in explaining the social organization of populations and species (Emlen and Oring 1977; Hayes *et al.* 2007; Wang *et al.* 2011).

While there have been important correlative and experimental studies that investigated the influence of food resources and population density on home range characteristics, it is not yet clear from many of these studies whether a decrease in home range sizes can be attributed to increased food availability or to increased

population density (Taitt 1981; Taitt and Krebs 1981), as they did not control for higher intruder pressure. It is particularly difficult to conclude from previous food supplementation experiments whether individual home ranges decreased because individuals chose to have smaller home ranges, or because increased competition by immigrants restrained them to smaller home ranges. It is unclear whether the observed variation in home range sizes in these studies was due to population density, food availability or a combination of both (Quirici *et al.* 2010; Maher and Burger 2011). Careful experimental manipulations of food availability and population density, including experimental controls and variation of one factor while keeping the other constant, could clarify the effects of each variable and demonstrate causation (Maher and Burger 2011).

In the present study we used an experimental approach to investigate the role that food availability and population density have on home range size and overlap in female African striped mice (*Rhabdomys pumilio*). We focused on females as territoriality in female mammals is thought to be related to the defence of critical food resources important for reproduction and survival, while male territoriality often functions to defend females and is thus a function of female home range sizes (Ostfeld 1985; Wolff 1993). Female African striped mice are territorial (Schradin 2004). In the Succulent Karoo, where we conducted our experiments, adult breeding female striped mice typically live in family groups. Each group normally consists of a breeding male, several breeding females and their philopatric offspring (Schradin 2004; Schradin and Pillay 2004). Individuals belonging to the same group have individual home ranges, but share one territory, which they defend aggressively against intruders (Schradin 2004; Schradin and Pillay 2004). Previous correlative studies have shown that home range sizes of females are influenced by seasonality, availability of food resources, cover, the number of direct neighbours and relative individual body mass, but not by population density (Schradin *et al.* 2010c). These conclusions were based on correlative observational data that need to be validated experimentally, while at the same time controlling for the effects of other environmental factors. Here, we used two separate controlled field experiments to assess the respective effects of food availability and population density.

In the first experiment, we provided food to 15 focal groups using experimental feeders. This experiment was conducted in a short time period of eight weeks. In

order to avoid an increase of population density as observed in previous food supplementation studies, groups at the boundaries and outside of the study area also received experimental food supplementation. We predicted that home range sizes of female striped mice would decrease when food was supplemented and would increase again once food was removed. In the second experiment, we decreased population density by removing some of the groups within the study area. We predicted that home range sizes of female striped mice would increase following the removal of their direct neighbouring groups. We performed the population density experiment within a short time period of seven weeks, to avoid a substantial decrease in the natural food availability and to allow sufficient time for detecting changes in home range parameters. As the number of direct neighbours represents a more accurate measure of being spatially constrained than population density (Schradin *et al.* 2010c), we also estimated the number of direct neighbours for each female. We predicted home range overlap with group members and with neighbours: i) to decrease when food was supplemented and to increase once food was removed; and ii) to decrease once neighbours were removed and population density became lower. Since female striped mice experience more aggression from neighbouring females rather than from neighbouring males (Schradin 2004; Schradin *et al.* 2010c), we predicted female neighbours to be significantly more influential than male neighbours in determining variation in home range sizes and overlap.

Habitat selection of individuals is often examined by comparing core area size to the total home range size (Rosalino *et al.* 2004; Dahl 2005; Kauhala and Auttila 2010). Core areas to home range sizes ratios show non-exclusive use of space and are thus important determinants of territorial behaviour (De Luca *et al.* 2010). We predicted core areas to home range sizes of female striped mice to: a) decrease when food was provided and to increase once food was removed; and b) to increase after the removal of individuals. Previous studied have shown that a reduction in home range size often correlates with both the experimental provisioning of supplemental food (Ims 1987; Hubbs and Boonstra 1998) and with the natural availability of food (Schradin *et al.* 2010c), thus, we wanted to test if a decrease in home range sizes due to supplemental food could be correlated with the natural availability of resources. Striped mice feed on both annual and perennial food plants (Schradin 2006; Schradin and Pillay 2006). Annuals are short-lived plants, which provide striped mice with high protein sources

and are important in determining the onset of the breeding season (Schradin and Pillay 2006). Perennial are long-lived plants, which are present throughout the year, and are an important food resource during the long dry summer (Schradin and Pillay 2006). Female striped mice home ranges are negatively correlated with both the amount of perennial and annual food plants (Schradin *et al.* 2010c), thus we predicted a reduction in home range sizes during the supplemental food experiment to be positively correlated with both the amount of perennial and annual food plants.

2. MATERIAL AND METHODS

(a) Study period and field techniques

Data were collected during the breeding seasons (August to November) of 2007-2010 on two separate field sites (29°42.30'S - 18°02.95'E) located near the town of Springbok in South Africa. Data for the feeding experiment were collected during the 2007 breeding season in the Goegap Nature Reserve, whereas data for the removal experiments were conducted during 2007-2010 breeding seasons at a field site located on the farm Klein Goegap, three km away from the field site where the food provisioning experiment was carried out. Data were gathered using a combination of trapping, radio-tracking and behavioural observations (Schradin *et al.* 2010a; Schoepf and Schradin 2012). All individuals occupying the same nest were regarded as belonging to the same group. Striped mice were trapped at their nest, sexed, weighed and their reproductive status was noted. Striped mice are considered adults when they reach sexual maturity at around 4-6 weeks of age and have a body weight of > 30g (Brooks 1982; Schradin *et al.* 2009a,b). For our study we only considered females that were already adults at the start of the experiment. To meet this criterion, females had to weigh 30g or more, to be older than six weeks and to show clear signs of reproduction (i.e. a female had given birth or was lactating). Therefore, the females that were included in the analysis were either born during the previous breeding season or early in the breeding season of sampling. To aid with individual recognition during behavioural observations, each trapped striped mouse trapped received permanent ear-tags (National Band and Tag Co., Newport, KY, U.S.A.) and was temporarily marked with a non-toxic hair dye (Inecto Rapido, Pinetown, South Africa). We used trapping data to identify focal females (those carrying a radio-

transmitter) as well as to determine the number of neighbouring males and females not carrying radio-transmitters (the nests of these neighbours were known from continuous observations and trapping at our field site).

Individuals were fitted with radio-collars (Holohil, Carp, Ontario, Canada) weighting between 1.2 and 4.5g. Radio-tracking data were collected using an AOR 8000 wide range receiver (Tokyo, Japan), an H-antenna (Africa Wildlife Tracking, Pretoria, South Africa) and a global positioning system (GPS; eTrex Venture, GARMIN International, USA) with an accuracy of ± 5m. Determination of home ranges was carried out by radio-tracking striped mice six times per day for a period of nine days using the same procedures outlined in previous studies (Schradin and Pillay 2005b; Schradin *et al.* 2010c). Radio-tracking was also carried out once at night to establish nesting sites locations and group composition (Schradin and Pillay 2005a).

(b) Food supplementation experiment

Resource availability was experimentally manipulated by supplying striped mice with protein-rich food directly in the field. Food (a mixture of sunflowers, corn and peanuts; Brenco, Tswana Feeds and Packaging, South Africa) was experimentally presented in an artificial feeder (Fig. 1). The feeder consisted of a plastic bottle with the top cut open and a hole in its side. The bottle was placed upside down in the field and was encased in a plastic container, which was fitted with a short opening tube (of approximately 15 cm), which allowed easy access for striped mice to the food and, at the same time, prevented birds or larger animals to access the supplemental food. We placed two feeders near each nest and positioned their opening towards the shrub. To control for population density and to prevent individuals living outside of the field site from immigrating into the study area, additional feeders were placed at the boundary and outside of the experimental area. Feeders were maintained throughout the experiments. Empty feeders were left in the field before and after food provisioning and refilled at regular intervals during food supplementation. We often observed striped mice entering or leaving the feeders. Frequency of visits to the feeders was estimated by calculating the number of points falling within a five meters radius of the feeder. Calculations were carried out using the software Map Source (Version 6.11.6, Garmin Ltd.). A total of 23 breeding females belonging to 15 different groups were

fitted with collars and radio-tracked throughout the experiment as described above. Females were radio-tracked for home ranges three times: 1. before the feeders were positioned in the field; 2. a week after the feeders had been placed in the field; and 3. a week after the feeders were removed. We recorded a total of 54 fixes for each individual during a home range. The adjustment time of one week was chosen to give females enough time to become accustomed to the presence and absence of food inside the feeders.

Figure 1.
An example of a feeder in the field. Note that during the experiment, the entrance into the box pointed towards and not away from the bush as shown in this picture. (Picture by G. Schmohl)

Previous studies in female striped mice have shown that home range quality is negatively correlated with home range size (Schradin *et al.* 2010c), thus, an increase in food availability may not influence the behaviour of females on high quality home ranges as much as the behaviour of females on low quality home ranges. We conducted plant surveys within each female home range to test whether a decrease in home range sizes due to supplemental food might also be correlated with the natural availability of resources. Plants surveys were conducted before the start of the experiment; to measure the amount of annuals and perennial food plant available. Over each home range, a 2x2 m grid was placed using a 30m measuring tape and at each 2m point the vegetation was assessed (for more details see Schradin *et al.* 2010c).

(c) Removal experiment

All striped mice sampled for the removal experiment were part of a field manipulation experiment in which we tested the role of population density on sociality by removing entire groups from the field site (for more details see Schoepf and Schradin 2012). Each removal experiment consisted of two replicates of six groups each: two groups were removed, two groups were monitored as experimental groups and two groups were used as control groups (Schoepf and Schradin 2012).

Before removal, all adult individuals belonging to each group involved in the experiment were fitted with radio-collars. A total of 159 adults (60 males and 99 females) were radio-tracked during the experiment. All individuals were radio-tracked for an initial period of nine days to establish home range sizes, composition of groups and to decide which group to remove (for more details see Schoepf and Schradin 2012). Removal of individuals took place immediately after radio-tracking for home ranges had ended. Individuals belonging to groups directly adjacent to groups that were removed were considered as experimental individuals because they experienced a direct decrease in the local population density. Individuals belonging to groups directly adjacent to the experimental groups but not the removal groups were considered as controls, because their local population remained the same or only declined slightly as a consequence of the dispersal of some of the experimental striped mice (Schoepf and Schradin 2012). A total of 13 breeding females were removed during the experiments and were thus not included in the study. Altogether, 47 breeding females from control groups and 39 breeding females from experimental groups were radio-tracked during the experiment. Females were radio-tracked for four weeks after removal, to allow sufficient time for detecting changes in home range parameters and to exclude for the study individuals that dispersed (see Schoepf and Schradin 2012). Three adult females belonging to experimental groups dispersed into the vacated areas after removal (Schoepf and Schradin 2012) and were excluded from the study. Predator pressure was significant at our field site (see Schoepf and Schradin 2012), with both control groups and experimental groups declining in size during the experiment. Altogether, 17 females belonging to 14 experimental groups and 31 females belonging to 16 control groups survived throughout the entire experimental study period of seven weeks and were considered for the final data analysis.

(d) Calculation of home range size and overlap

Home range sizes and overlap were calculated using 100% minimum convex polygon (MCP; Mohr 1947) and 100% kernel contours (KC; Worton 1989) methods with the software Ranges6 (Anatrack Ltd, Wareham, U.K.). We report data obtained by using MCP methods to facilitate comparisons with previous studies on striped mice (Schradin and Pillay 2004; Schradin and Pillay 2005b; Schradin *et al.* 2010c). KC methods are increasingly favoured (Matthiopoulos 2003; Barg *et al.* 2005; Börger *et al.* 2006b) and are included here to allow comparisons with other species. 95% MCP and KC were calculated to exclude the influence of potential outliers on home range sizes, whereas 50% MCP and KC were used to estimate core areas (e.g. Ostfeld 1986; Hubbs and Boonstra 1998). Core areas were peeled around the kernel centre, which indicates the location with the highest density (Samuel *et al.* 1985; Worton 1989). Overlap were calculated to detect: a) shifts in area use between home ranges before and after experiments; and b) to measure areas shared between target individuals, their group members (intra-group overlap) and their neighbours (extra-group overlap). Overlap were determined using the 100% MCP and 100% KC methods by calculating the area in common between the home ranges of two females. To give an indication of space use, average ratios of core areas to home range sizes were calculated before, during and after food was provided (experiment 1), and before and after individuals were removed (experiment 2).

(e) Estimation of population density and the number of neighbours

Population density was calculated by dividing the size of the area occupied by all the adults (> 6 weeks old) belonging to all the groups involved in the experiments. Solitary roamers (i.e. non-territorial solitary-living adults; Schradin and Pillay 2004) often have larger home ranges than territorial breeders (Schradin *et al.* 2009a) and could have visited females belonging to groups not included within the study area, thus they were excluded from any population density calculations. For the removal experiment, population density was calculated both before and after individuals were removed. The number of neighbours was calculated for each focal female separately by counting all roaming males or group-living adult individuals whose home range was a maximum of 30m away from the home range of the focal female.

(f) Data analysis

Data analysis was performed using the statistical software R (version 2.11.0 R Development Core Team 2006). Data were tested for normality using the Shapiro-Wilk Normality Test and are presented as mean ± standard error. Home range sizes (100% MCP, 95%MCP and 95%KC) were log-transformed prior to analysis. Repeated measures ANOVA followed by a paired t-test with Bonferroni correction were used to compare home range sizes and overlap of the same individual before, during and after the food supplementation experiment. Pearson correlation coefficients (r) were calculated to test for correlations between: a) variation in home range size (calculated as the ratio between home range size during the food supplementation experiment and home range size before the food supplementation experiment) and the relative amount of annual plants measured before food was supplemented; and b) variation in home range size and the relative amount of perennial food plants.

Paired t-tests were used to test home range size of control and experimental females before and after the removal of individuals. To test for the effect of population density on home range size we used a linear mixed effect models (LMM). Home range size was treated as the response variable and population density was treated as the fixed factor. As population density in our study embeds group size (see Chapter 1 for more details), we did not include group size as a separate variable. We selected the model that best fitted our data by using Akaike's Information Criterion (AIC; following Crawley 2007). We verified our model selection by plotting the model residuals *versus* the fitted values; by checking the normal distribution of the model residuals using normal probability plots and by checking for heteroscedasticity and leverage (Crawley 2007). In a second LMM, we tested for the effect that the presence of other members of the group had on females' home range sizes. Home range size was treated as the response variable while presence/absence of the group breeding males and number of breeding females (zero or more than one) were included as the fixed factors. A third LMM was used to test for the effect of the number of neighbours on female home range sizes. Home range size was treated as the response variable and the number of neighbouring breeding males, breeding females and roaming males was included as the fixed factors. Individuals ID, group and replicate (see page 36 for more details) were included as random factors in each LMM. Only two-way

interactions were considered in the models. Home range sizes were log-transformed prior to analyses owing to their right-skewed distribution. We used unpaired t-test to compare whether differences in home rage sizes of females before and after removal of individuals were due to the presence or absence of either other breeding females or the breeding male of the group. We used Wilcoxon Sign-Rank Tests with exact p-value calculation to compare overlap before and after removal of individuals of control and experimental females with other female and male group-members, and with neighbouring breeding females, breeding males and roamer males.

3. RESULTS

(a) The effects of resource availability

Kernel centres of females home ranges were close to feeder positions (individuals were radio tracked 18.17 ± 2.48% in the bush adjacent the feeder) indicating that feeders were frequently used. Visits to the feeders varied significantly before, during and after food supplementation (ANOVA, $F_{2, 22} = 6.67$, $p = 0.003$), with females spending significantly less time visiting the feeders after, rather than before, the experiment (paired t-test, $t = 3.91$, $p = 0.002$). Differences between visits to the feeders before and during the experiment and during and after the experiment, respectively, were however not significant (paired t-test, before and during: $t = 2.01$, $p = 0.11$; during and after: $t = 1.47$, $p = 0.15$).

Female home range sizes calculated using 100% MCP varied significantly before, during and after food was supplemented (0.29 ± 0.04ha *vs.* 0.21 ± 0.02ha *vs.* 0.27 ± 0.03ha, ANOVA, $F_{2, 22} = 4.19$, $p = 0.02$). Home range sizes significantly decreased when food was supplemented (paired t-test, $t = 2.72$, $p = 0.04$; Fig. 2) and show a non-significance tendency to increase when food was removed (paired t-test, $t = 2.22$, $p = 0.09$; Fig. 2). Home range sizes did not differ before and after the food manipulation experiment, indicating that home ranges of individual females returned to sizes originally occupied once the supplemental food was removed (paired t-test, $t = 0.51$, $p = 0.70$; Fig. 2). Females home range sizes calculated using 95% KC also significantly varied before, during and after food was provided (ANOVA, $F_{2, 22} = 3.56$, $p = 0.04$), in particular, significantly decreasing when food was supplemented

(paired t-test, t = 2.42, p = 0.04; Fig. 2), and tending to increase after food was removed (paired t-test, t = 2.18, p = 0.07; Fig. 2). Home range sizes did not differ before and after the food manipulation experiment (paired t-test, t = 0.24, p = 0.84; Fig. 2). Females home range sizes calculated using 95% MCP only tended to vary before, during and after food was provided (ANOVA, $F_{2, 22} = 2.88$, p = 0.07; Fig. 2). Core area size significantly varied before, during and after food was provided (50% MCP: ANOVA, $F_{2, 22} = 3.44$, p = 0.04; 50% KC: ANOVA, $F_{2, 22} = 5.26$, p = 0.009; Fig. 2). Core area size significantly decreased when food was supplemented (50% MCP: paired t-test, t = 2.03, p = 0.05; 50% KC: paired t-test, t = 2.91; p = 0.008; Fig. 2), and increased once food was removed (50% MCP: paired t-test, t = 3.13, p = 0.005; 50% KC: paired t-test, t =3.57; p = 0.002; Fig. 2).

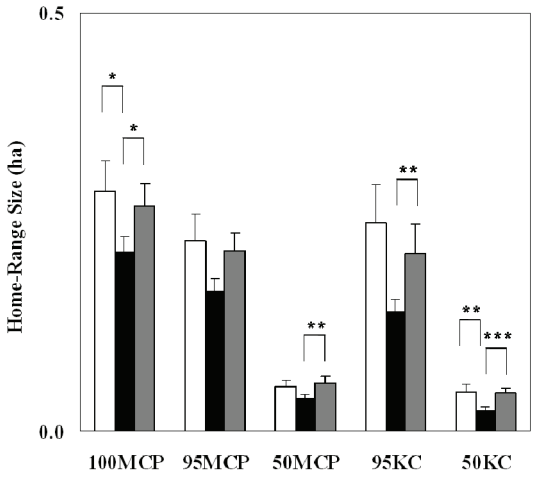

Figure 2.
Overview of home range sizes and core area sizes (Mean ± StEr) of female striped mice before (white), during (black) and after (grey) food supplementation using 100%, 95% and 50% MCP and 95% and 50% KC methods (n = 23). * p <0.05, ** p <0.01.

The ratio of core areas to home range sizes remained similar before, during and after food supplementation for 50% MCP / 100% MCP (before: 0.20 ± 0.01ha; during: 0.19 ± 0.02ha; after: 0.22 ± 0.02ha; ANOVA, $F_{2, 22} = 1.67$, p = 0.20) and 50% MCP / 95% MCP (before: 0.26 ± 0.02ha; during: 0.24 ± 0.02ha; after: 0.27 ± 0.02ha; ANOVA, $F_{2, 22} = 0.83$, p = 0.44). However, we found a difference in the ratio of core areas to home range sizes before, during and after food supplementation for 50% KC / 95% KC (before: 0.20 ± 0.01ha; during: 0.17 ± 0.02ha; after: 0.22 ± 0.02ha; ANOVA, $F_{2, 22} = 4.14$, p = 0.02), which tended to decrease when food was provided (paired t-test, t =

1.95, $p = 0.06$) and increased significantly when food was removed (paired t-test, t = -2.39, $p = 0.05$).

Females showed a high degree of overlap with their own home range before, during and after the food supplementation experiment (ANOVA, $F_{2, 22} = 0.27$, $p = 0.77$), indicating that females did not shift their home range into different areas when additional food was provided but mostly used the same area over time.

Female striped mice did not show any significant difference in their home range overlap with other female group-members (ANOVA, $F_{2, 37} = 0.25$, $p = 0.78$), or with extra-group individuals before, during or after food was provided (ANOVA, $F_{2, 11} = 0.55$, $p = 0.59$).

Reduction in home range sizes due to food provisioning was positively correlated with relative availability of annual plant species found within the home range of an individual (Pearson correlation: n = 23, r = 0.51, $p = 0.01$; Fig. 3), but not with relative amount of perennial food plants (Pearson correlation: n = 23, r = -0.09, $p = 0.69$).

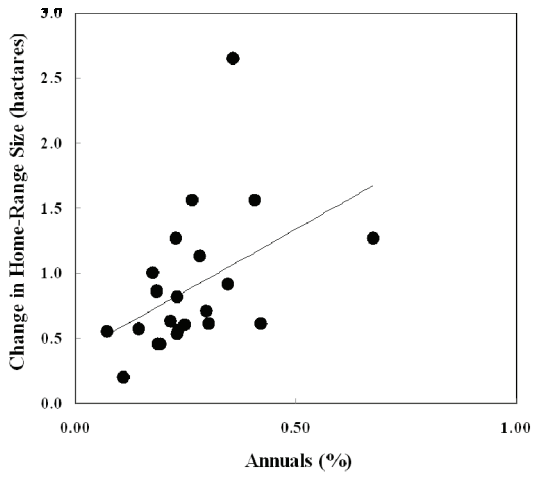

Figure 3.
Correlation between home range size variation (calculated as the home range size during the experiment divided by the home range size before the experiment) of female striped mice and relative amount of annual plants measured in their home range before the experiment. Each point represents a female striped mouse (n = 23).

(b) The effects of reduced population density and the number of neighbours

Home range size of experimental females did not differ from those of control females before (100% MCP: unpaired t-test, $t_{46} = 0.94$, $p = 0.35$; 95% MCP: unpaired t-test, $t_{46} = 0.89$, $p = 0.37$; 95% KC: unpaired t-test, $t_{46} = 0.15$, $p = 0.88$) and after removal of individuals (100% MCP: unpaired t-test, $t_{46} = 1.29$, $p = 0.20$; 95% MCP: unpaired t-test, $t_{46} = 0.41$, $p = 0.68$; 95% KC: unpaired t-test, $t_{46} = 0.06$, $p = 0.95$). This was mainly due to home range size of both control and experimental females significantly increasing after individuals were removed (100% MCP; control: 0.39 ± 0.04ha *vs.* 0.50 ± 0.04ha, paired t-test, $t_{30} = 3.56$, $p = 0.001$; experiment: 0.45 ± 0.06ha *vs.* 0.63 ± 0.09ha, paired t-test, $t_{16} = 2.84$, $p = 0.01$; 100% KC; control: paired t-test, $t_{30} = 2.70$, $p = 0.01$; experiment: paired t-test, $t_{16} = 2.72$, $p = 0.02$; Fig. 4a, b). Home range size of control females increased significantly also when these were calculated using 95% MCP and 95% KC method (95% MCP: paired t-test, $t_{30} = 3.84$, $p = 0.001$; 95% KC: paired t-test, $t_{30} = 3.21$, $p = 0.003$; Fig. 4b) . Home range size of experimental females showed a non-significant tendency to increase when these were calculated using 95% MCP and 95% KC method (95% MCP: paired t-test, $t_{16} = 1.86$, $p = 0.08$; 95% KC: paired t-test, $t_{16} = 1.89$, $p = 0.08$; Fig. 4a).

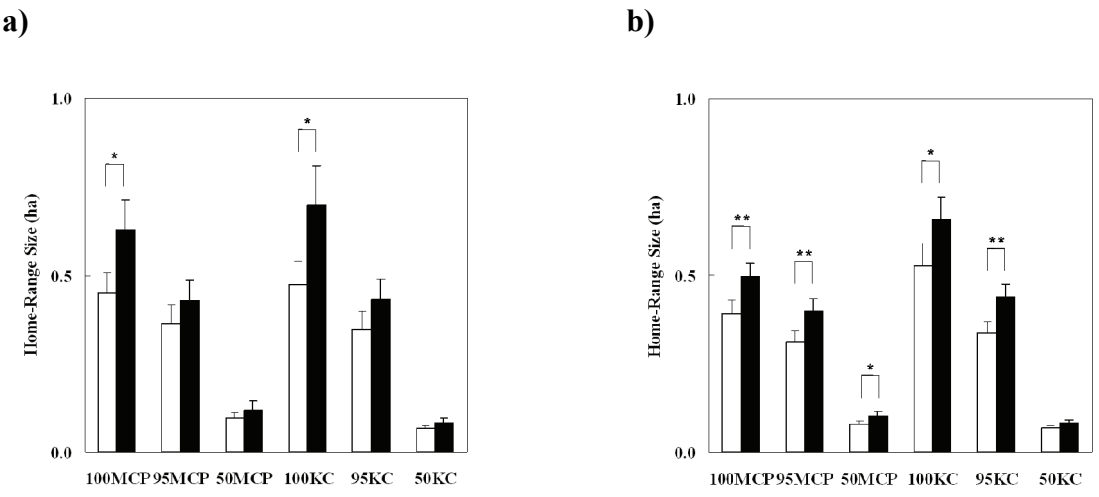

Figure 4.
The home range size and core area size (Mean ± StEr) of female striped mice before (white), and after (black) removal of individuals using 100%, 95% and 50% MCP; and 100%, 95% and 50% KC methods. a) Data from experimental females (n = 17). b) Data from control females (n = 30). * $p < 0.05$, ** $p < 0.01$.

Mean core area to home range size ratio of control and experimental females remained similar before and after removal of individuals for 50% MCP / 100% MCP (control: 0.22 ± 0.01ha *vs.* 0.21 ± 0.01ha, paired t-test, $t_{30} = 0.68$, $p = 0.50$; experiment: 0.23 ± 0.02ha *vs.* 0.18 ± 0.02ha, paired t-test, $t_{16} = 1.48$, $p = 0.16$); 50% MCP / 95% MCP (control: 0.27 ± 0.02ha *vs.* 026 ± 0.02ha, paired t-test, $t_{30} = 0.64$, $p = 0.53$; experiment: 0.28 ± 0.02ha *vs.* 0.25 ± 0.02ha, paired t-test, $t_{16} = 0.71$, $p = 0.49$) and 50% KC / 95% KC (control: 0.21 ± 0.01ha *vs.* 0.19 ± 0.01ha, paired t-test, $t_{30} = 1.56$, $p = 0.13$; experiment: 0.21 ± 0.02ha *vs.* 0.19 ± 0.02ha, paired t-test, $t_{16} = 0.82$, $p = 0.42$).

Home ranges of individual females after removal overlapped greatly with their own home range before the removal of individuals (Control: 63.98 ± 3.26%; Experiment: 56.98 ± 4.49%), indicating that experimental and control females used mostly the same area when other individuals were removed. Experimental females did not differ in the overlap with their previous home range from control females (unpaired t-test, $t_{46} = 1.26$, $p = 0.21$).

Home range sizes increased significantly when local population density decreased because of the removal of individuals (LMM: $F_{2, 46} = 9.09$, $p = 0.0005$; Fig. 5a). The presence and number of other breeding females within the group negatively affected home range size of females (LMM: $F_{2, 44} = 6.06$, $p = 0.005$). After removal of individuals, home range sizes of females associated with one or more breeding females significantly increased (unpaired t-test, $t_{77} = 2.44$, $p = 0.02$; Fig. 5b). Home range sizes of females that had no other breeding females within their group remained similar before and after removal of individuals (0.42 ± 0.14 *vs.* 0.58 ± 0.13; unpaired t-test, $t_{15} = 1.01$, $p = 0.33$). The presence of the breeding male positively affected home range sizes of females (LMM: $F_{2, 44} = 7.33$, $p = 0.002$). In particular, after removal of individuals, only home range sizes of females associated with a breeding male significantly increased (unpaired t-test, $t_{86} = 2.96$, $p = 0.004$), but not of females without a breeding male (unpaired t-test, $t_6 = 1.15$, $p = 0.29$; Fig. 5c). The number of neighbouring breeding females affected the size of a female's home range negatively (i.e. as the total number of neighbouring females decreased following removal of individuals, female home range sizes increased; LMM: $F_{2, 42} = 4.37$, $p = 0.02$, Fig. 5d). The number of neighbouring breeding males and roamer males tended to affect the size of a female home range negatively (i.e. as the total number of neighbouring

breeding males and roamers decreased following removal of individuals, female home range sizes showed a non-significant tendency to increase; neighbouring breeding males: LMM: $F_{2, 42} = 2.66$, $p = 0.08$; roamers: LMM: $F_{2, 42} = 2.57$, $p = 0.09$).

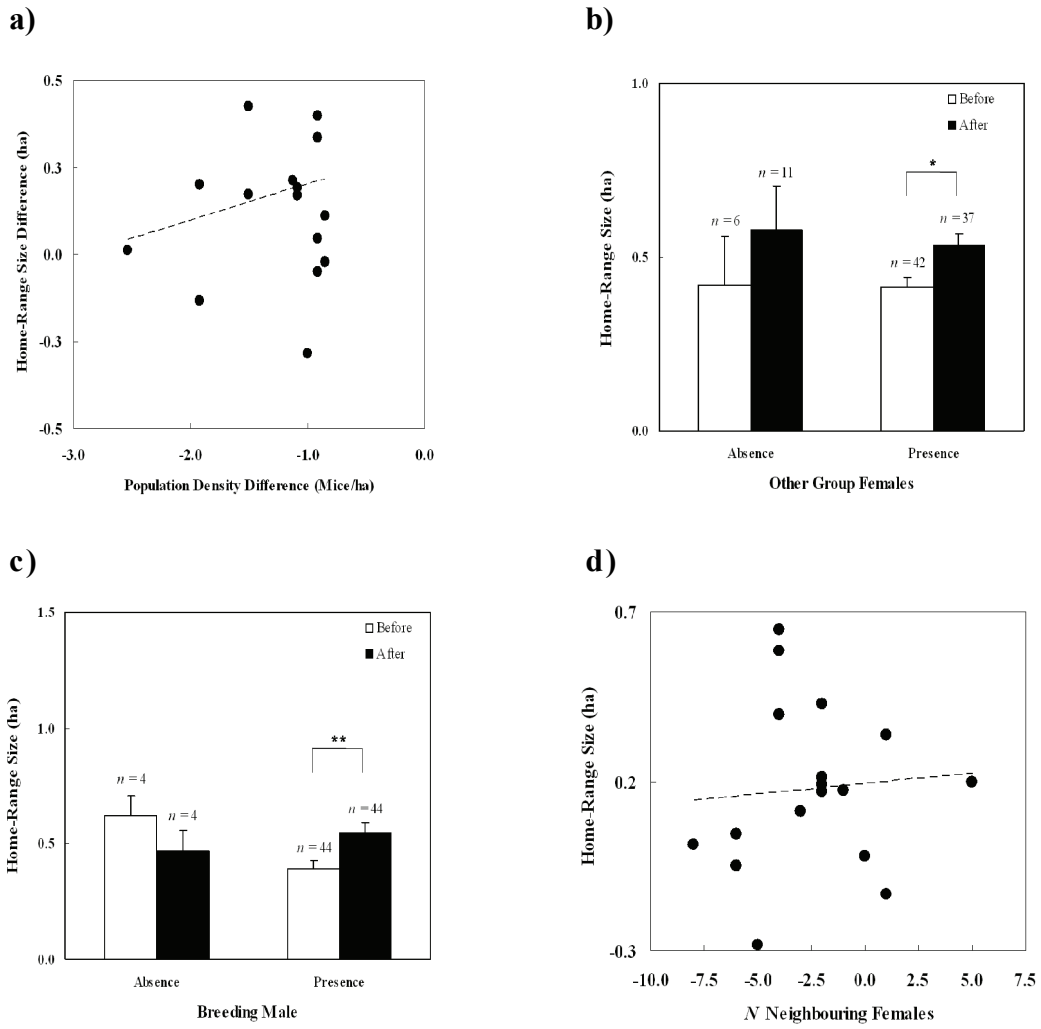

Figure 5.
Home range sizes of female striped were: a) positively affected by a reduction in population density (after-before values in home range size and population density are plotted in the graph); b) negatively affected by the number of breeding females within the group; c) positively affected by the presence of the breeding male of the group; and d) negatively affected by the number of neighbouring females (after-before values in home range size and population density are plotted in the graph). Each point represents one of the experimental female (n = 17).

Before and after removal of individuals, experimental females showed a significant decrease in their mean overlap with neighbouring roamer males (Wilcoxon-Sign Rank Test, n = 17, V = 148, $p = 0.001$, Fig. 6), and a trend towards decreasing their mean

overlap with neighbouring breeding males (15.49 ± 9.64% *vs*. 3.82 ± 8.06%; Wilcoxon-Sign Rank Test, n = 17, V = 105, p = 0.06). Females did not show any significant difference in their overlap with other female group-members (37.70 ± 9.17% *vs*. 23.92 ± 8.55%; Wilcoxon-Sign Rank Test, n = 17, V = 18, p = 0.38); with the breeding male of their own group (32.81 ± 7.90% *vs*. 36.39 ± 7.75%; Wilcoxon-Sign Rank Test, n = 17, V = 51, p = 0.38) or with neighbouring breeding females (14.46 ± 2.68% *vs*. 16.28 ± 2.90%; Wilcoxon-Sign Rank Test, n = 17, V = 71, p = 0.90). Before and after removal of individuals, control females did not show any significant difference in their overlap with other female group-members (47.12 ± 4.68% *vs*. 25.65 ± 5.55%; Wilcoxon-Sign Rank Test, n = 31, V = 143, p = 0.18); with their breeding male (28.84 ± 5.27% *vs*. 35.70 ± 5.04%; Wilcoxon-Sign Rank Test, n = 31, V = 248, p = 0.32); with neighbouring breeding females (14.09 ± 3.15% *vs*. 10.70 ± 1.83%; Wilcoxon-Sign Rank Test, n = 31, V = 143, p = 0.42); with neighbouring breeding males (11.98 ± 1.99% *vs*. 11.79 ± 2.05%; Wilcoxon-Sign Rank Test, n = 31, V = 181, p = 0.63); or with roamers (11.07 ± 2.44% *vs*. 8.08 ± 1.63%; Wilcoxon-Sign Rank Test, n = 31, V = 107, p = 0.23).

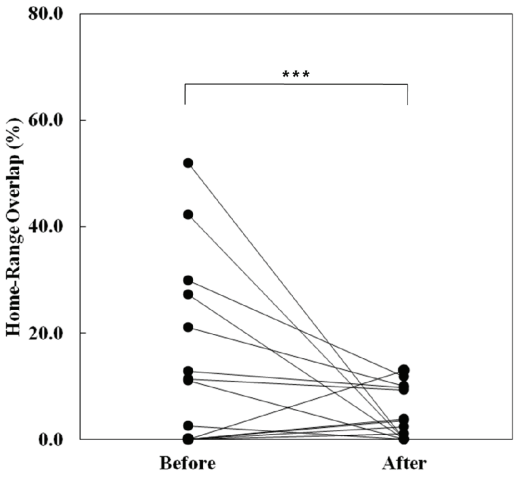

Figure 6.
Experimental striped mouse females significantly increased the area they overlapped with a) neighbouring breeding males; and b) roaming males significantly after population density was experimentally decreased. Data of single females are connected by a line (paired data; neighbouring breeding males: n = 13; roaming males: n = 9).

4. DISCUSSION

Many correlative studies have shown home range sizes to be negatively correlated with resource availability and with population density, but experimental tests of these two factors are rare and characterized by the difficulty that food availability and population density are normally positively correlated. Ours is the first study where both factors were tested experimentally and independently of each other. As predicted, we demonstrated a causal influence of both food availability and population density on home range sizes. When supplemental high protein food was provided, female home ranges decreased by approximately 25%, whereas when individuals were removed from neighbouring territories female home ranges increased by approximately 40%. Taken together it appears that competition with neighbouring individuals rather than resource availability is the key factor determining space use patterns in female striped mice. Females showed a high percentage of overlap with their own home range throughout the food supplementation and the removal experiments, indicating that females used the same area over time. Overlap with other female group-members and neighbours remained similar throughout both experiments, suggesting that female striped mice tend to minimize encounters with other females even when the size of their home range increases. The presence of the breeding male positively influenced home range sizes of females and females decreased their overlapping areas with neighbouring males, particularly with roaming males, suggesting that males might play a more important role than previously thought in affecting females space use patterns.

(a) The effect of resource availability

Home ranges of female striped mice decreased when food was provided and increased to levels similar to those recorded before the start of the experiment a week after the supplemental food was removed. Our results concur with previous studies in other species, which showed that individuals decreased their home ranges when additional food was made available (Enoksson and Nilsson 1983; Ims 1987; Roth and Vetter 2008), and that their centres of activities got closer to the site where food was provided (Roth and Vetter 2008). However, in previous studies data were collected over long periods of time and did not control for the correlative effects of increased

population density due to increased immigration and recruitment by reproduction (Taitt and Krebs 1981; Enoksson and Nilsson 1983; Roth and Vetter 2008). In contrast, our study was conducted over a much shorter period, with data collected within five weeks after onset of food supplementation, a period during which no immigration was observed. To avoid immigration, we also provisioned neighbouring groups that did not take part in the study with feeders. Our study was, however, conducted during the breeding season and even though our experiment was conducted over a short period, an increase in population density through reproduction might have nonetheless occurred. Even so, larger adult breeders can easily dominate juveniles (Schradin 2004), so competition with younger individuals could have not have caused the reduction in home range sizes we observed, particularly as females increased their home ranges to sizes similar to those they occupied at the start of the experiment once the supplemental food was removed. We conclude that the variation in home range sizes observed during our experiment was caused by food supplementation and not by an increase in population density due to reproduction.

While the distribution and quality of available resources will vary seasonally in seasonal environments (Forman 1995), it has been suggested that individuals might need extra resources to meet the increased energy demands associated with reproduction during the breeding season (Liu *et al.* 2009). In many mammals, female reproductive success is highly dependent on body condition (Dreiss *et al.* 2010; Schradin *et al.* 2010c), and it is expected that females will increase their home ranges to secure additional resources (Wang *et al.* 2011), which might induce conflict with neighbouring individuals. Indeed, numerous field studies have shown that the frequency of intraspecific aggression increases when food availability decreases (Stamps and Buechner 1985; Eberhard and Ewald 1994; Luna and Baird 2004). Female striped mice in our study significantly changed the sizes of their home ranges, but did not show any significant change in their overlap with either female group-members or with neighbouring females. This suggests that competition for food resources with neighbouring individuals did not increase when supplemental food was available, in contrast to findings in other species that showed an increase in home range overlap when additional food was provided (Ostfeld 1986; Ims 1987). However, in these studies females were spatially clumped, whereas we were able to avoid such effects by placing our feeders systematically in the field and not randomly.

Thus, our study provides one of the best controlled field experiments conducted to demonstrate that the availability of food causally influences home range size in female mammals.

Resource distribution within an individual's home range may determine both its size and use (Börger *et al.* 2006a). When extra food was provided, females with a low proportion of annuals within their territory decreased their home ranges more than females with high proportions. Females that inhabited better quality territories had overall smaller home ranges than females that inhabited lower quality territories, which might thus have benefitted more from an increase in the availability of extra-food. A reduction in home range sizes during the experiment did not, however, correlate with the availability of perennial plants, indicating that annuals are more important food sources than other plants. Annual food plants are important sources of protein-rich food for striped mice and their appearance during the rainy season induces breeding in this species (Perrin 1980). Annuals may be important year-round for striped mice since it has been shown that even in the non-breeding season, individuals shift their home ranges to include more annual plants (Schradin and Pillay 2006).

(b) The effects of reduced population density and the number of neighbours

Population density correlates negatively with home range sizes (Fortier and Tamarin 1998; Priotto *et al.* 2002; Luna and Baird 2004), and several studies have shown that when neighbours are experimentally removed or have disappeared, the remaining individuals increase their home range sizes (Norman and Jones 1984; Boutin and Schweiger 1988; Baker *et al.* 2000). In accordance with this, female home range sizes in our study significantly increased after we decreased local population density by removing their neighbours. However, following the removal of individuals, we observed an increase in home range sizes not only in females belonging to experimental groups, but also in females of control groups, whose direct neighbours were not removed. The enlargement of home range sizes of control females might be explained in terms of reduced population density by natural predation. Predator pressure can significantly affect the use of space of a prey species with increased predation often being associated with larger prey home ranges (Maher and Burger

2011). Studies on degus (*Octodon degus*) have, for instance, shown that individuals in predator free areas concentrated their foraging activities in smaller patches where food was most abundant because the population size of degus in these areas was greater (Lagos *et al.* 1995). At our field site, predator pressure was significant (see Schoepf and Schradin 2012), with both control groups and experimental groups declining in size due to mortality caused by birds of prey, mammals and reptiles. Because of predation, even individuals belonging to control groups experienced, though to a lesser degree, a decline in the local population density, which can thus explain why even control females were able to increase their home range sizes.

After the removal of individuals, home ranges of both control and experimental females overlapped greatly with their own home range before the removal of individuals. Furthermore, the size of their core areas remained similar throughout the experiment, indicating that females used mostly the same area even when their neighbours were removed and their home ranges increased. Females might attempt to monopolize additional resources, which could be used both for their own reproduction and for their weaned offspring that remain within their mother's home range for a long period after reaching adulthood (Schradin *et al.* 2010c), as it is easier to defend rather than acquire a new territory (Hammerstein 1981).

Female striped mice home range sizes were influenced by the presence and number of other breeding females in the group. In fact, as more space became available, females, which shared their nest with other breeding females, significantly increased their home range size. Space sharing among female mammals is thought to be possible due to kin selection favouring amicable interactions among relatives (Dobson 1982; Le Galliard *et al.* 2006; Rosell *et al.* 2008). However, intra-group conflict with other breeding females can be a major cost of sociality (Danchin *et al.* 2008). In the Succulent Karoo, striped mice live in groups (Schradin and Pillay 2004), which typically consists of related communally breeding females that share a nest and a territory, but forage alone (Schradin and Pillay 2005b; Schradin 2006). Intra-group conflicts among female striped mice can be high and mostly occurs in the form of aggression and infanticide (Schradin *et al.* 2010a). Given the opportunity (i.e. the availability of increased space and resources) female striped mice sharing the nest with other breeding females might try and reduce the costs associated with intra-group conflicts arising from resource competition by enlarging their own home range

whenever possible. From here it would follow that an increase in home range sizes would correspond to a decrease in overlapping areas with other female group members, yet in our study this was not the case, maybe because females help each other in territory defence (Schradin 2004). Cooperation among females has been shown to be more important than competition in different prairie dogs species (Hoogland 2013), and could also be the case in striped mice. By huddling together at night striped mice benefit from increased thermoregulation, significantly reducing energy expenditure and water consumption: benefits, which are particularly important for survival in a semi-desert environment (Scantlebury *et al.* 2006). Home range and non-exclusiveness among breeding female striped mice group members may thus be primarily related to the benefits of group-living which are maintained even when individuals enlarge their own home range.

Strikingly, the home range size of a female striped mouse was positively influenced by the presence of the breeding male of its own group. Traditionally, female territoriality is linked to the distribution of resources, while males' territoriality is mainly linked to the distribution of females (Emlen and Oring 1977; Ostfeld 1985), so that male mammals are usually more territorial and defend larger areas than females (Rosell *et al.* 2008). In Mongolian gerbils (*Meriones unguiculatus*), the home range size of a social group is positively related to the body mass of the largest male (Ågren *et al.* 1989). Male striped mice show more patrolling behaviour than females (Schradin 2006), although their home ranges are not larger than those of breeding females (Schradin and Pillay 2004, 2005b). Thus female striped mice might benefit from the territorial behaviour of their breeding males when increasing their own home range, as the breeding male assists its female in defending her territory. On the other hand, when females increase their home range, their breeding males might also have to increase their own to defend the area covered by their females and to avoid their females mating with other males, as, extra-group paternity can be quite high in striped mice (36%; Schradin *et al.* 2010b).

The presence of neighbouring breeding females affected a female home range size negatively, which may have been a result of females competing directly for the same resources (Schradin *et al.* 2010c). During the breeding season, the energy requirements of females increase due to the costs associated with gestation and lactation (Degen *et al.* 2002; Liu *et al.* 2003). To secure more resources to raise their

offspring, females may try to enlarge their own home range (Hoset *et al.* 2008). If a female lives in close proximity to other females, they will meet frequently in aggressive territorial encounters (Stamps and Buechner 1985; Luna and Baird 2004). Thus, pressure from neighbours may cause individuals to compress their territory below its optimal size (Maynard-Smith 1974; Patterson 1985). In a previous correlative study on home range sizes of female striped mice, heavier breeding females with better competitive abilities were able to occupy larger home ranges (Schradin *et al.* 2010c). As individuals were experimentally removed in our study, females were able to enlarge their home ranges due to relaxed pressure from neighbours. Our results concur with previous studies in striped mice (Schradin *et al.* 2010c) showing that females with many neighbours have smaller home ranges than females with few neighbours.

Several previous studies in other species have shown that home range overlap with neighbours tended to decrease or even disappear at low densities (Lambin and Krebs 1991; Hoset *et al.* 2008; Wang *et al.* 2011). Female striped mice in our study did not show a decrease in overlapping areas with neighbouring females following the removal of individuals from the study site. While home range sizes of all females increased significantly, increasing the likelihood of an increase in overlap with neighbouring individuals, the encounter rate with neighbours decreased, because there were fewer female neighbours in total (the total number of breeding females in the study site decreased from 119 to 88). Yet, this alone cannot explain why female striped mice significantly decreased their overlapping areas with roaming males after the removal of individuals, as the number of roaming males also decreased following removal (the total number of roaming males in the study site decreased from 26 to 15). Studies in root voles (*Microtus oeconomus*) and other small mammals showed females to be more defensive against aggressive unfamiliar conspecifics, in particular infanticidial males, than familiar ones (Agrell *et al.* 1998; Ebsensperger 1998; Le Galliard *et al.* 2006) rather than neighbours (Rosell *et al.* 2008). Female striped mice might perceive roaming males to be more of a threat to their offspring than neighbouring breeding males and thus have decreased their overlap with them given the opportunity (i.e. when vacant territories are available). As population density decreased, breeding males also had fewer male competitors (the total number of breeding males in the study site decreased from 53 to 47), and could have thus

become more capable of keeping other males, especially lighter and less competitive roamers (Schradin 2004; Schradin *et al.* 2009a; Schradin and Lindholm 2011) away from their own females.

(c) Conclusions

It has long been suggested that the most important predictors of home range sizes and overlap of females are food availability and population density or a combination of both. However, most experimental studies of home range sizes and overlap have focused on only one of these two factors without accounting for the other, even though it is widely known that they correlate significantly with each other. We addressed the role that resource availability and population density play on home range sizes and overlap through two separate controlled field experiments. In the first experiment we manipulated resource availability, by providing additional food, and controlled for the correlative effects of population density; founding a reduction in home range sizes of approximately 20%. In a second experiment, we investigated the effects of population density, by removing neighbouring individuals, and controlled for the effects of food availability and seasonality by limiting the experiment to a relatively short time during the breeding season, founding an increase in home range sizes of approximately 40%. By focusing on a single sex (female) and social category (breeding adults), our study additionally controlled for a potential age- and sex-dependent density effect on home range sizes and overlap. Our experimental study supports the hypothesis that variation in home range sizes and overlap is governed both by the availability and quality of resources as well as by population density, yet the latter appears to have a more prominent role in influencing space use patterns: females are more prone to increase their home range when free space is available than to decrease their home range when food is unlimited.

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GENERAL DISCUSSION

GENERAL DISCUSSION

The aims of my thesis were to identify the ultimate and proximate factors that lead individual striped mice to either remain group-living or to disperse and become solitary. I approached this topic by looking at the environmental, the behavioural and the physiological aspects of group- versus solitary-living. I began by investigating the environmental reasons that would lead individuals to choose one social tactic over the other. I showed that individuals become solitary to avoid reproductive competition, but remained group-living when ecological constraints were high and when reproductive competition was absent. I demonstrated that group-living striped mice differ in their social behaviours from solitary individuals, and that these differences were already present before individuals became solitary. Further, I was able to show that group-living individuals differ physiologically from solitary individuals. In particular, they retained higher corticosterone levels and lower testosterone levels than solitary individuals, indicating that avoiding reproductive suppression is the reason leading to solitary-living in this species. Finally, I examined how the availability of food resources and population density affected space use patterns of group-living individuals, and showed that, while both are important, population density is the major factor affecting space use in striped mice. In sum, using an experimental approach I tried to demonstrate causation of several concepts that previously were mostly described using correlative and observational studies.

1. ULTIMATE AND PROXIMATE REASONS OF SOCIALITY: AN INTEGRATIVE APPROACH

Understanding the extent that environmental factors bear on individuals' behaviour is crucial in determining how the environment influences the social organization of populations and species (Emlen and Oring 1977; Hayes *et al.* 2007). Several studies have, for example, shown that the spacing behaviour of individuals is correlated with multiple ecological constraints. For example, home range size can be negatively correlated with food availability (Tufto *et al.* 1996; Travis and Slobodchikoff 1993; Saïd *et al.* 2005), indicating that when food is scarcer individuals need more space to meet their energetic requirements. Additionally, a large home range that includes a large amount of resources may lead to higher personal fitness, thus, an individual

should aim to secure enough resources for itself and its offspring (Stamps 1994; Adams 2001; Lopez-Sepulcre and Kokko 2005). However, an area that includes a large number of resources may also attract several competitors and the provisioning of additional food in some experimental studies also attracted immigrants and resulted in an increase in the local population density (Taitt and Krebs 1981; Hews 1993; Perrin and Johnson 1999). Due to the highly correlative nature of these two factors (i.e. food availability tends to decrease as population density increases), it has been so far difficult to determine which ecological constraint is the most important in affecting the home range of an individual. I tested independently for the role that population density and availability of resources play on space use patterns of female African striped mice (*Rhabdomys pumilio*) by using two separate field manipulation experiments, in which I varied one of the two factors and kept the other constant. In accordance with previous studies I was able to show a causal influence of both food availability and population density on home range sizes (Ims 1987; Luna and Baird 2004; Roth and Vetter 2008). In contrast to previous findings, however, I found that female striped mice did not shift their home range but mostly used the same area throughout the study. Striped mice females' home range sizes and overlap were not influenced by the number of other female group-members, which may be related to the benefits of group-living that are maintained even when individuals enlarge their own home range. The number and the sex of neighbouring individuals also significantly affected home range sizes and overlap of females. The presence of neighbouring breeding females, in particular, affected a female home range size negatively, which could have been due to the fact that females compete directly for the same resources (Schradin *et al.* 2010b). My results concur with previous studies in striped mice (Schradin *et al.* 2010b) and several other species showing that females with many neighbours decrease their home range sizes and overlap (Lambin and Krebs 1991; Hoset *et al.* 2008; Wang *et al.* 2011). These two experiments support the hypothesis that the availability and quality of resources is an important factor determining variation in home range sizes and overlap, but population density is the most important determinant of space use patterns in African striped mice (**Chapter 4**).

Population density is a critical factor that determines not only the way an individual uses its space, but it is also important in determining its sociality. Using a field

experiment, in which I manipulated population density by removing groups of striped mice, I showed that when population density was high and all the territories were occupied, individuals remained group-living. However, as territories became available and local population decreased, philopatric striped mice belonging to experimental groups dispersed and became solitary (**Chapter 1**). My results support the "habitat saturation hypothesis" (Emlen 1982; Hatchwell and Komdeur 2000) and the findings from several previous experimental studies (Dickinson and McGowan 2005; Griesser *et al.* 2008).

While ecological constraints are important in maintain group-living, they could not explain why striped mice only dispersed and became solitary during the breeding season. During the non-breeding season, striped mice remained group-living, even when vacant territories were available, suggesting that besides population density additional factors play a more prominent role in determining solitary-living in this species. The main difference between the breeding- and the non-breeding season was whether or not breeding and thus reproductive competition occurred: reproductive competition can thus be seen as the main factor driving solitary-living in African striped mice (**Chapter 1**).

At the environmental level, reproductive competition may be seen as the ultimate limiting factor determining dispersal and solitary-living in striped mice, but at the individual level, the physical, physiological and behavioural attributes specific to an individual may be crucial in determining whether it disperses or remains group-living. For example, it has been suggested that striped mice might choose to either disperse or to remain group-living depending on when they are born and reach sexual maturity during the breeding season (Schradin *et al.* 2010a). It is expected that individuals that are born early have more chances of establishing their own territory than individuals that are born late in the season when conditions are no longer optimal. Individuals that are born earlier experience a higher abundance of food resources, which accelerate their development, and thus explains why older and heavier individuals can become solitary roamers while younger and smaller males remain philopatric, and why only the heaviest and older individuals in our experiment, and not all, became solitary when conditions were favourable (**Chapter 2**).

Dispersal might be thus dependent on the age and body mass of an individual, but also on the specific traits in its behavioural phenotype, which could explain why I observed high variation in dispersal tendencies within striped mice of similar age and body mass. Behavioural traits such as exploration, aggression, and sociability may influence the chances of individuals to survive and reproduce in a new environment. Striped mice that dispersed and became solitary were more aggressive and more investigative than striped mice that remained group-living. Striped mice that became solitary were already more aggressive and more investigative than mice that remained group-living before dispersal (**Chapter 2**). These results corroborate with previous studies, which showed that more aggressive individuals are more likely to disperse (Myers and Krebs 1971; Kaplan *et al.* 1995; Howell *et al.* 2007) and that the tendency to show more exploratory behaviour may develop already before dispersal (Holekamp 1986; Cote *et al.* 2010; Hoset *et al.* 2011).

Individuals with specific personalities might experience lower costs of dispersal than other individuals, facilitating their settlement in a new area (Clobert *et al.* 2009). Several studies have shown a link between dispersal tendencies and different behaviours, such as aggression, exploration and sociability (Clark and Ehlinger 1987; Sih *et al.* 2004; Bell 2007). I found that the most aggressive, the most explorative and the least sociable mice were the most aggressive, the most explorative and the least sociable even after they changed tactic. The behaviour of dispersing mice was consistently different from the behaviour of mice that remained group-living, thus suggesting that differences in personality traits may influence dispersal probabilities and ultimately affect the fitness of an individual (**Chapter 2**).

It thus seems that it is ultimately the environment (i.e. presence or absence of reproductive competition and of free territories) that determines whether individuals with the most suitable personality (i.e. the most aggressive and most investigative individual) can disperse and become solitary. This idea is further supported by my physiological findings (**Chapter 3**), which showed that individuals that became solitary decreased their corticosterone levels and males – but not females –increased their testosterone levels. In group-living species, competition over space and resources may be intense and can result in parents and more dominant individuals suppressing subordinates (Blumstein and Armitage 1999, Saltzman *et al.* 2006). In striped mice, the dominant breeding male of the group is thought to reproductively

suppress its philopatric sons (Schradin *et al.* 2009b). Thus dispersing and becoming solitary may be a tactic chosen to avoid suppression and harassment by the adults (Andreassen and Gundersen 2006; Le Galliard 2006; Le Galliard *et al.* 2007).

Together with the findings from **Chapter 1** where I showed that more male striped mice that dispersed and became solitary were scrotal (indicating they were physiologically ready to mate) than males that remained group-living; and females that became solitary had a higher reproductive success than females that remained philopatrics, the hormonal results presented in **Chapter 3** indicates that individuals that dispersed and became solitary were successful in reducing reproductive competition and thus in escaping reproductive suppression.

Reproductive suppression brought about by the presence of the dominant breeders leads to increased glucocorticoids levels and decreased androgens levels in subordinates (Creel 2001; Wingfield and Sapolsky 2003; Schradin *et al.* 2009a; Schradin *et al.* 2012). Striped mice of both sexes that became solitary had significantly lower corticosterone levels than individuals that remained group-living, suggesting that adopting a solitary tactic can be a way to avoid social stress arising from living in a group. It has been suggested that in striped mice corticosterone might suppress testosterone (Schradin *et al.* 2009a; Schradin and Yuen 2011) and in my study males that left their natal group to become solitary had increased testosterone levels, while males that remained group-living retained high corticosterone levels and low testosterone levels (**Chapter 3**). These results support the assumption that philopatric males are physiologically and reproductively suppressed.

In sum, only when environmental conditions are favourable (i.e. when ecological constraints are relaxed), group-living individuals that reach a certain competitive ability (i.e. heavier and older) and have a specific personality are able to escape reproductive suppression and adopt a solitary tactic (Fig 1.). The switch from group-living to solitary is accompanied by behavioural and hormonal adjustments that may allow the disperser to maximize its survival probability and enhance its fitness in the new environment (Fig 1.).

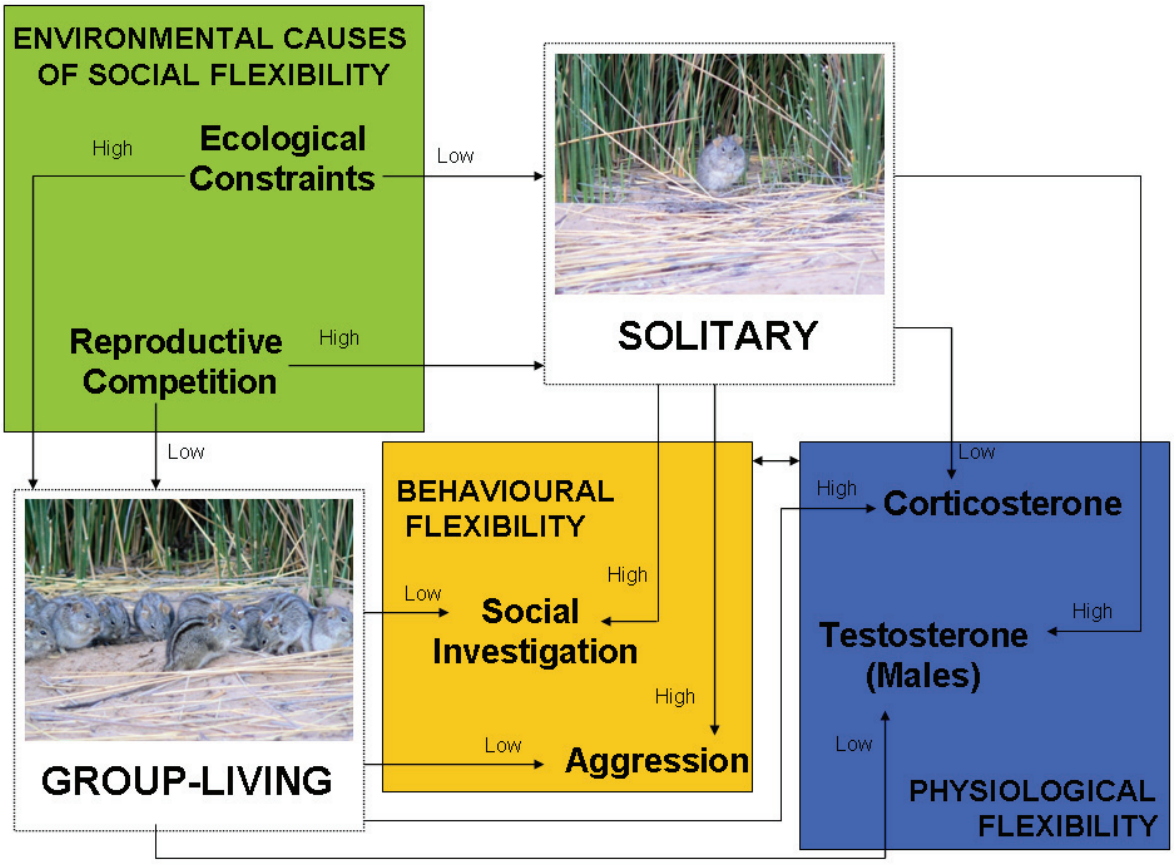

Figure 1.
Graphical representation of the ultimate and proximate factors leading to a switch from a group-living to a solitary-living social tactic. The model shows the environmental causes of social flexibility (green box); the behavioural adaptations/predispositions (yellow box) and physiological mechanisms (blue box) resulting from a switch in the social tactic. Each factor can either occur at high or low levels.

2. CONCLUSIONS

Solitary and group-living species are expected to differ in the way they react to environmental constraints, yet comparisons of proximate and ultimate causes for group- versus solitary-living are very rare. Our understanding of sociality and how it evolved and is maintained has been constrained by our ability to address the ultimate and the proximate factors that lead to group- and solitary-living. So far, this could only be achieved by comparing several species with different social organizations. In my research I was able to overcome this constraint by comparing the ecological, behavioural and physiological profiles using a single socially flexible species, the

African striped mouse. My research provides experimental evidence of previous correlative results obtained for striped mice (Schradin *et al.* 2010a). To my knowledge, this is the only research that simultaneously looked at exogenous (i.e. environmental) and endogenous (i.e. behavioural and physiological) factors determining sociality by using an experimental approach. Specifically, mine is the first experimental field study that provides empirical evidence that ecological constraints, and, in particular, population density, not only influence space use in group-living individuals but also the sociality of a species. While ecological constraints are important determinants of sociality, reproductive competition within groups is the ultimate factor that induces solitary-living. Few other studies have examined the potential relationship between behaviour expressed within the social context and its repercussion on the social organization of a species. Taken together these results demonstrate that there is a link between environmental change, behavioural adaptation and underlining physiological mechanisms, which result in significant fitness consequences depending on whether individuals adopt a group-living or a solitary life.

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